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THE NORTHERN FLINT CORNS

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The slender-eared, wide-kernelled flint corns of New York State and New England were for centuries (see Table III) the commonest type of maize in eastern North America. As dent varieties pushed northward and as earlier and earlier varieties of dents have been developed, these wide-seeded flints have been restricted to an ever-narrowing fringe along the northern edge of maize cultivation. Today they are of secondary economic importance but their role in the production of the very varieties which supplanted them makes their study imperative to the modern corn-breeder. In addition to their intrinsic interest as a well-marked and formerly widespread type of *Zea Mays*, their close identification with the Indians of the eastern United States renders their history and relationships of compelling interest to the American archaeologist.

During 1944-46 a collection of these northern flint varieties was brought together and grown in the experimental plots of the Pioneer Hi-Bred Corn Company, at Johnston, Iowa. We are especially indebted to Dr. R. G. Wiggans of Cornell University for suggesting sources of seed for a number of eastern varieties.

Tables I and II list the varieties by name, in so far as this was known, and their places of origin. A photographic record was made of one plant of each collection, and herbarium specimens were prepared of two or more tassels (male inflorescence). Internode diagrams (Anderson and Schregardus, '44) were made of representative plants, and the following record was made of the tassels: tassel branch number, condensation index (Anderson, '44), number of tertiary branches, presence of whorling in the central spike, and number of paired spikelets per whorl. Open-pollinated ears were obtained from each culture and were scored for cob and kernel color, kernel width, kernel thickness, amount of denting, and diameter of the shank below the ear. These various scores and measurements are presented in Tables I and II.

For cytological study, sporocytes from each of the varieties were killed and fixed in 3 parts alcohol to 1 part propionic acid. After 24 hours at room temperature they were stored in a refrigerator until they were smeared in propionic carmine. Chromosome knob numbers were obtained from each culture. The results are tabulated in Tables I and II and are discussed in detail below.

MORPHOLOGY

It was immediately apparent that, in spite of much plant-to-plant variation, the northern flints were essentially homogeneous at the eastern end of their range in New York and New England but became increasingly variable as the Great Plains were approached. This is equally true whether one considers the morphology of the plants, the appearance of the ears, or the knob numbers of the chromosomes. This is also true of the extensive archaeological material which has been examined and which is described later in this report. The following description therefore applies to the relatively uniform material from the Northeast. As shown in Table II, similar varieties are also found in the northern Great Plains but there they are accompanied by other kinds of flint corns (pls. 3 and 4).

The ears of the northeastern flints are characteristically long and slender with 8 to 10 rows of wide, crescent-shaped kernels (pls. 1, 2). The cob is strong and proportionately large, particularly toward the base, and the shank or ear-stalk is thick and well-developed. Frequently the base is noticeably larger than the rest of the ear, and even in those varieties which do not exhibit this character in a prominent fashion, a tendency in this direction may be seen in increased row numbers, irregular kernels, or irregular rowing at the base of the ear. This increased basal development in the northeastern flints is most conspicuous when comparisons are made with 8-rowed varieties from western Mexico and with some of the flints of the southwestern United States. Such varieties taper toward the base instead of becoming increasingly wider.

As might be expected, the northeastern flints are of early maturity. They have more suckers or tillers than the common dent varieties from the same area, and these tillers are usually shorter than the main stalk and often bear malformed ears and tassels. Prop-roots are less common than in United States dent varieties; there are usually very few above the level of the soil surface. The culms are small and slender with long internodes and are lighter green than most dent varieties. The leaves are narrow and the ears are borne on long shanks. The leaves of the ear shoot (the husks) have conspicuous blades (fig. 4) which are sometimes referred to as "flag-leaves" by sweet-corn breeders. The combination of slender culms, irregular tillers, and well-developed flag leaves gives all these flints a distinctive general aspect.

The tassels of the northeastern flints are wiry and open. Tassel branch numbers are mostly from 12 to 16. There is little or no condensation (fig. 2), and the spikelet pairs are thinly and evenly spaced along the secondary branches. The tassels have a slender axis with long internodes. The central spike is thin and

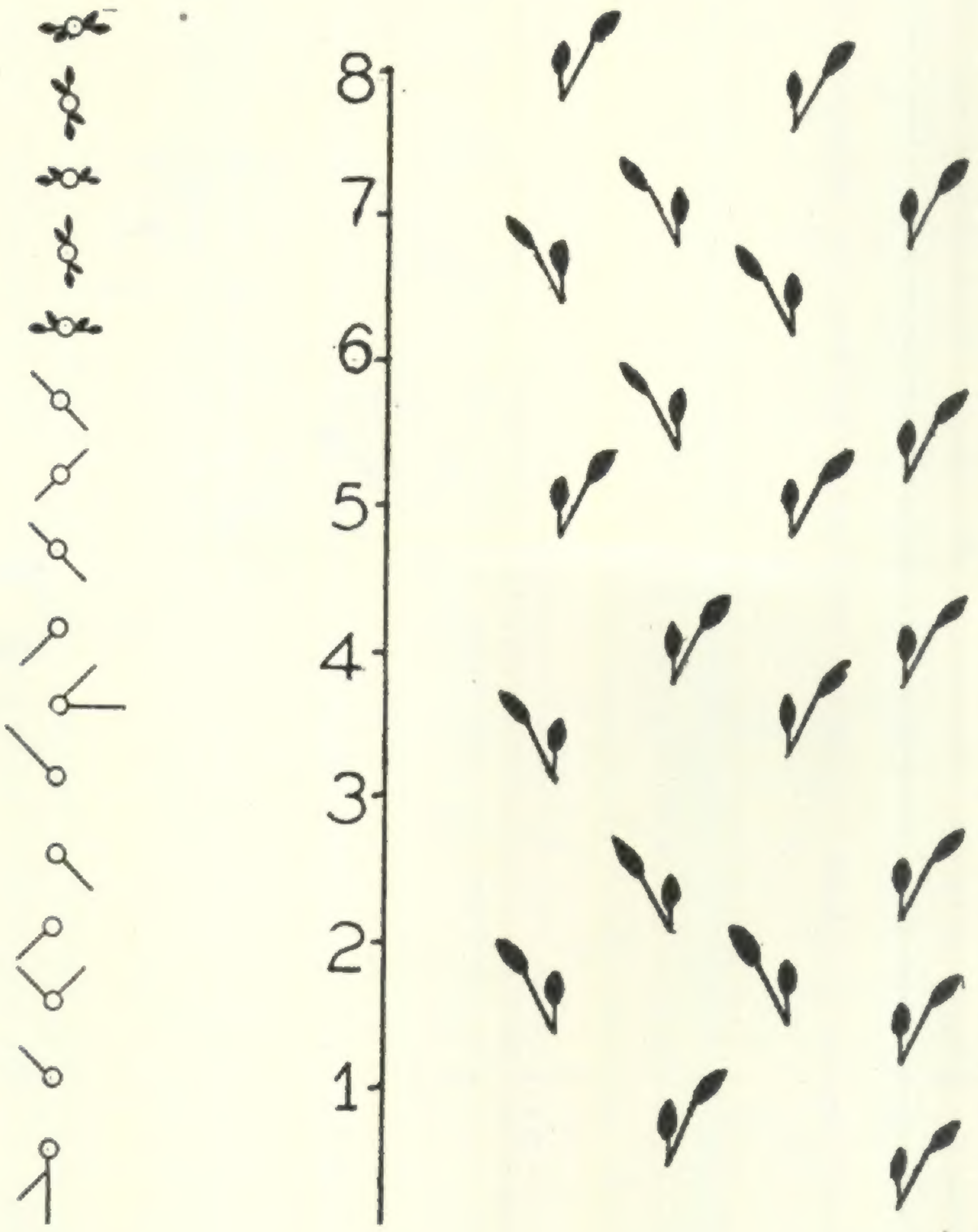


Fig. 1. Actual diagram showing branching pattern and spikelet arrangement of a typical tassel of Longfellow Flint. Left: the 11 nodes of the branched portion of the tassel, showing the number of branches at each node (in this case 1 or 2) and the approximate direction in which they pointed. Immediately above these 11 nodes are the first 5 nodes of the central spike, each of which bore 2 pairs of spikelets. Right: a diagram to scale of the actual position of all the spikelets on an 8-cm. section of the central spike. The technique is adapted from that used by Mangelsdorf ('45) and represents a portion of the spike as if it had been slit down one side and flattened out from a cylinder to a rectangle. Scale at left in cm. All the spikelets in this specimen were in pairs, one member of each pair being sessile and one pedicellate. All were in 4 ranks and, aside from 1 extra pair at the lower right-hand corner, were arranged 2 pairs to a node, the pairs being at right angles to the next nodes above or below; in other words, decussate, which means that if there were spikelet pairs at the north and south ends of a particular node, those at the next node would be on the east and west sides, those at the second node at the north and south again, etc.

without the conspicuously thickened central portion so characteristic of most dent corns and certain varieties of popcorn. The arrangement of the tassel branches is more regular than appears from casual observation. In those varieties which are mostly 8-rowed it is as follows: The upper two branches are opposite and below

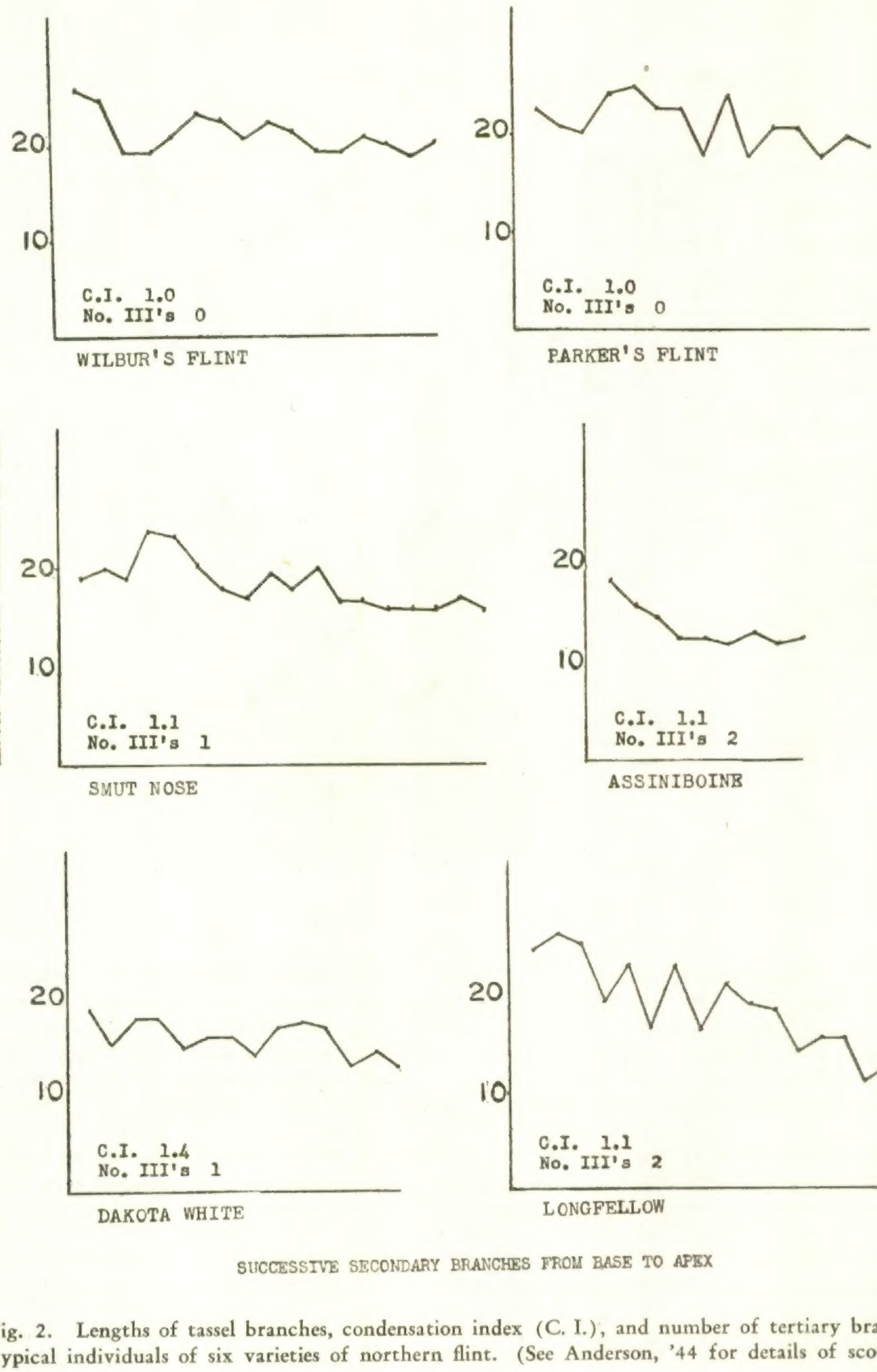


Fig. 2. Lengths of tassel branches, condensation index (C. I.), and number of tertiary branches for typical individuals of six varieties of northern flint. (See Anderson, '44 for details of scoring.)

them is a series of branch pairs which are opposite or practically so. Toward the base of the tassel these pairs become increasingly indistinct until finally there is a single branch at each node. The lower two branches are usually 2-ranked and on opposite sides of the axis though well separated. There is a strong tendency for the tassel branches, as a whole, to be quite regularly 6-ranked but aside from this we have been able to find no general regularity in the way they are arranged on the stem, which varies between the clearly opposite pair just below the central spike and the alternately 2-ranked pair at the base of the tassel. Detailed records of a typical tassel are presented in fig. 1.

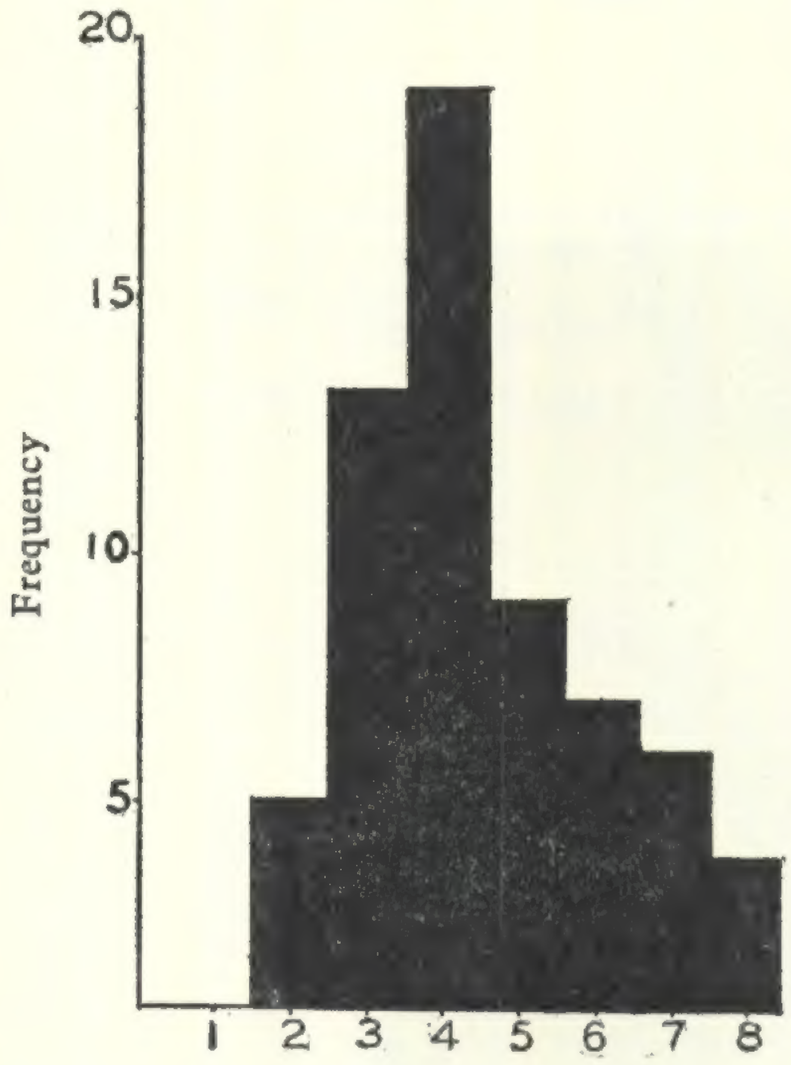


Fig. 3. Frequency distribution of chromosome knob numbers in dent corn inbreds.

The arrangement of the central spike is surprisingly simple and does not seem to have been previously described. In the 8-rowed crescent-seeded flints it is clearly whorled. At each node there are two pairs of spikelets, one of each pair being pedicellate and one sessile. The pairs at each node are at right angles to those immediately below and immediately above, so that the spike, as a whole, is 4-ranked and decussate. This simple arrangement is somewhat masked by a slight twisting of the axis, and in some plants by a low degree of multiplication (Cutler, '46, p. 269). In 10- and 12-rowed varieties the patterns may be modified in various ways. If there is enough condensation (Anderson, '44) to telescope some of the nodes on the secondary branches, there may be additional spikelets at the nodes, or the clear division into nodes may not be apparent and the spike will seem to be arranged spirally instead of being whorled. In some of the Plains flints with 12-rowed ears the central spikes may be whorled but the whorls have three spikelet pairs instead of two as in the 8-rowed varieties.

TABLE I
VARIETIES FROM THE NORTHEAST

Variety	Source	Cob color	Kernel color	Kernel thickness (cm.)	Kernel width (cm.)	Denting*	Diam. shank (cm.)	Number of rows	Number of chromosome knobs**
Canada Flint	Feeding Hills, Mass.	White	Yellow, purple	.46	1.0	0	1.4	8	0
Dutton	Newark Valley, N. Y.	White	Yellow, purple	.40	1.0	0	2.1	8	2
Harris Mammoth Yellow	Rochester, N. Y.	White	Yellow	.44	1.1	0	1.6	8	0
Longfellow	Ontario	White	Yellow	.41	1.0	0	1.5	8	1
Mammoth Yellow	Ithaca, N. Y.	White	Yellow	.38	1.0	0–1	1.6	8	2
Parker's Flint	Potsdam, N. Y.	White	Purple, red, yellow	.44	1.0	0	1.1	8	0
Quebec Flint	Restigouche, Que.	White	Yellow	.20	.5	0	.8	8–10	1
Smut Nose	Bath, N. Y.	White	Yellow, red	.48	1.0	0	1.7	8	2
Stevens	Ithaca, N. Y.	White	Yellow, red	.41	1.1	0	2.4	8	0
Thayer Flint	Searsport, Me.	White	Yellow	.44	1.0	0	1.9	8	0
Thompson Flint	East Andover, N. H.	White	Yellow, red	.45	1.0	0	1.4	8	0
12-row Red Flint	Dryden, N. Y.	White	Yellow, red	.40	.9	0	2.1	12	1
12-row Yellow Flint	Dryden, N. Y.	White	Yellow, red	.44	.8	0	1.6	12	0
Wilbur's Flint	Hudson Falls, N. Y.	White	Yellow	.50	1.0	0	1.4	8	0

* 0—no denting or visible soft starch; 1—visible soft starch; 2—slight dent.

** Numbers do not include organizer knob on chromosome 6.

TABLE II
VARIETIES FROM THE GREAT PLAINS AND THE MIDWEST

Variety	Source	Cob color	Kernel color	Kernel thickness (cm.)	Kernel width (cm.)	Dent-ing*	Diam. shank (cm.)	Number of rows	Number of chromosome knobs***
Argentine Flint**	North Dakota	White	Yellow, white, purple	.44	1.0	0	2.1	8–12	1
Assiniboine	North Dakota	White	Yellow, white, purple, red	.44	.9	0–1	1.2	8	1
Dakota Squaw	North Dakota	White	Yellow, white, purple, red	.46	.9	0–1	1.9	10	1
Dakota White	North Dakota	White	Yellow, white, purple	.42	.9	1	2.1	8–10	0
14-row Dakota Flint	South Dakota	White	Yellow, white, purple, red	.46	.9	0	2.3	14	0
Gehu	North Dakota	White	Purple, yellow	.40	.8	0–1	1.9	8–12	0
Gehu	Iowa	White	Yellow	.44	.7	0	1.9	12	2
Harris Mammoth Yellow	Iowa	White	Yellow	.51	1.0	0	1.6	8	0
Longfellow	Madison, Wis.	White	Yellow, purple	.41	1.2	0	1.7	8–10	1
Mandan & Arikara	North Dakota	White	Red	.43	1.0	0	1.2	8	5
Mercer County Flint	North Dakota	White	Yellow, purple	.42	.8	0	2.1	8–10–12	0
Rainbow	North Dakota	White	Yellow, purple	.42	.8	0–1	1.5	12	1
Russian Extra Early	North Dakota	White	Yellow	.36	.6	0	1.2	8–12	2
Russian Extra Early	Wisconsin	White	Yellow	.44	.7	0–1	.9	12	2
Russian Extra Early	Iowa	White	Yellow, purple	.40	.6	0	1.5	12	3
Sac & Fox	Tama, Iowa	White	White, purple	.40	.9	0	2.2	8	—
Santee	North Dakota	White	Yellow, purple, white	.42	.9	0	1.9	12	0
Smut Nose	Madison, Wis.	White	Yellow, red, purple	.50	.9	0	1.6	8	1
Spanish Pop	Ames, Iowa	White	Yellow, white	.42	.7	0	1.1	8	0
12-row Dakota Flint	South Dakota	White	Yellow, white, purple, red	.47	.9	0	2.1	12	3
Winnebago	North Dakota	White	Purple, yellow	.40	1.0	0	1.8	8	1
Zuni Blue	North Dakota	White	Purple, yellow, white	.44	1.0	2	2.1	12	5

* 0—no denting or visible soft starch; 1—visible soft starch; 2—slight dent.
** So called but probably contaminated with northern flint varieties.
*** Numbers do not include organizer knob on chromosome 6.

TABLE III

SUMMARY OF COLLECTIONS OF PREHISTORIC OR PROTOHISTORIC MAIZE IN VARIOUS MUSEUMS

State	Site	Museum	Number of rows					Kernel width in mm.								Remarks
			8	10	12	14	16	6	7	8	9	10	11	12	13	
New York	Alhart, Monroe Co.	R**								1	1			2	1	Crescent seeds. Prehistoric Iroquois
New York	Sackett Co.	R	20	2												"Owasco"*
New York	Kahler, Livingston Co.	R										1				"Owasco". Crescent seeds
New York	Castle Creek, Broome Co.	R									1	3	1			"Owasco". Crescent seeds
New York	Silver Wheels	H	1	1								1	1			
Ohio	Kettle Hill, Lancaster Co.	O	60	14	3											Shanks medium to large
Ohio	Canter's Cave	O		1	2	3										Also one 4-rowed freak. Straight-rowed
Ohio	Gartner Village	O	1						1	3	1		1			"Fort Ancient"
Ohio	Baldwin Village, Lancaster Co.	O&M	1									1				Crescent seeds Strong row pairing
Ohio	Fuert	M	3	4	2											Crescent seeds. "Fort Ancient"
Ohio	Baum	M&F	4	.					1	2	3		1			1500–1700
Ohio	Madisonville (Mound)	N	5	1	1						1	4	3			No denting "Owasco"
Michigan	Gibralter, Wayne Co.	M	2													Strong row pairing; big shank
Illinois	Kincaid (near Ohio R.)	M								2						
Illinois	Cable Site	M		1	3											
Illinois	Fisher	M							1	1						
Kentucky	Kings Mound (Wickliffe)	A	1		2	2			6	5	3	1				
Tennessee	Norris Basin 2322	M		1												
Tennessee	Norris Basin 2247	M													3	Wide crescent seeds
Tennessee	Norris Basin 2215	M		1						1						
S. Carolina	McDowell Mound, Kershaw Co.	N	6	9												Protohistoric pottery
Georgia	Stallings Mound, Columbia Co.	H	13	14												
Alabama	Guntersville Basin, TVA	M	6	15	1					1	3	2	1			Strong row pairing. Crescent seeds

TABLE III (Continued)

State	Site	Museum	Number of rows					Kernel width in mm.								Remarks
			8	10	12	14	16	6	7	8	9	10	11	12	13	
Iowa	Near Glenwood	A			2	2							1			No denting
S. Dakota	Rygh Site	M	1	3												Ear elliptical, widest above base
S. Dakota	Leavenworth	M	All													
S. Dakota	Elk Creek	M	1													Historic Arikara. Strong row pairing
Nebraska	Ponca Fort	M	All													Strong row pairing
Nebraska	Hill Site	M										1	1	1		
Nebraska	Near Lynch, Boyd Co.	M	2	3												Ear widest above base. Late prehistoric
Kansas	Tobias Site, Rice Co.	N	2	2	5	1			1	8	1					Mid 16th century
Kansas	Doniphan Site, Doniphan Co.	N	2	4	1											Post European; mid 18th century
Kansas	Fanning Site	N	1									1				
Missouri	Steed-Kiska, Platte Co.	N	2	1	2											No row pairing. Ear tapers both ways; from a cache pit
Missouri	Jane, McDonald Co.	M	—	—	—	—***					1	4				Smooth dimpled dent. White bluff rock shelter
Arkansas	From caves in N.W. Arkansas	M		2	4											No row pairing
Arkansas	From caves in N.W. Arkansas	A					1		1							No denting

* While archaeologists disagree as to dates, "Owasco" is definitely pre-Iroquois.

** Museums indicated by the following abbreviations: R—Rochester; H—Peabody-Harvard; O—Ohio State Museum; M—Museum of Ethnobotany, University of Michigan; N—National Museum; A—Ames; F—Chicago Museum of Natural History (Field).

***8–14 rows were found.

CYTOLOGY

The northeastern flints make excellent cytological material; as compared to most other United States varieties they are easy to smear and yield a high percentage of good preparations. This is, in part at least, the result of their being knobless or essentially so, that being the outstanding cytological feature of these corns. A summary of chromosome knob numbers for flints from the Northeast and from the Northern Plains is presented in Tables I and II. It will be seen that, aside from the organizer knob on chromosome 6, the northeastern flints are knobless or have only one or two knobs. The organizer knob is never large as in some Central American varieties. On the contrary, it is usually extremely small, light-staining and inconspicuous (fig. 5). The knob positions in the northern flints are also characteristic, as had previously been reported by Longley ('38) for the varieties of the northern Indians. When knobs are present in these varieties they are usually either small and terminal on chromosome 9 or two small knobs on the long arm of chromosome 6. The form of the terminal knob on chromosome 9 is also characteristic. It may be more or less cleft at the apex, or it may taper to an acuminate point; it is never large and cylindrical as in certain varieties from western Mexico. In all cases knobs in the northern flints are small; often they are only slightly larger than a large chromomere.

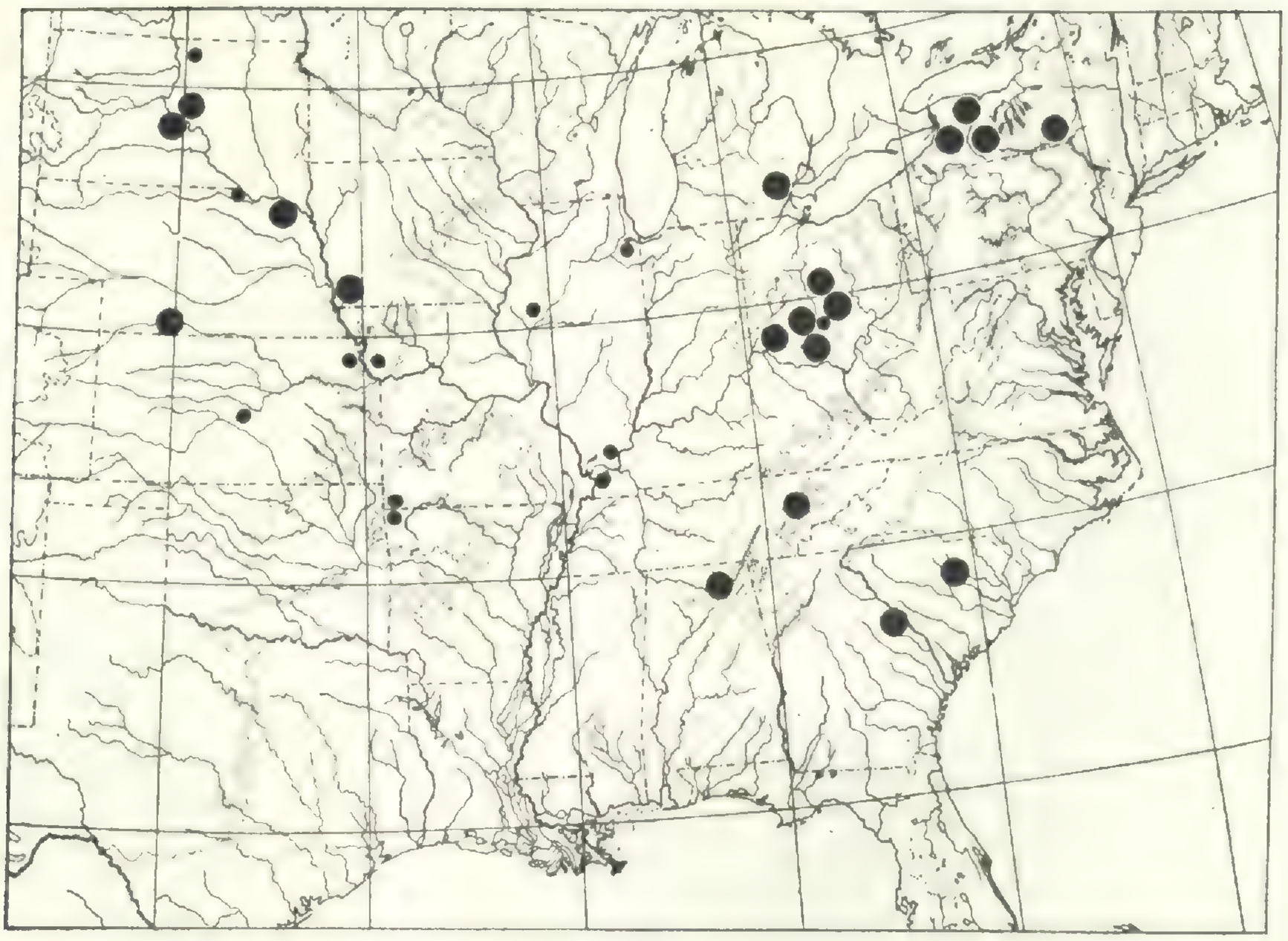
Since the varieties included in this study were from open-pollinated seed and were more or less heterozygous one might expect knob numbers to vary considerably within varieties. Actually the variation is slight, usually not more than one knob. Where different knob numbers were observed the number listed represents the average of a number of counts. Among the varieties examined cytologically, two (Parker's Flint and Twelve-row Dakota) were found to contain, in addition to the normal chromosome complement, one and two pairs of B chromosomes. The B chromosomes in the variety "Twelve-row Dakota" were unusually large and the pairs were frequently joined at pachytene of meiosis.

ARCHAEOLOGY

The rapid advances of American archaeology in the last few decades have added greatly to our knowledge of the history and development of maize. As additional collections of prehistoric material become available and as cultural sequences are more accurately determined, the history of corn in North America will no longer be a matter for argument. It will instead come within the domain of measurement as various collections are recorded and carefully compared with one another. For the northern flint corns, while some details remain to be filled in, the outlines of the story are already clear. They are shown in map 1 and a detailed report is presented in Table III. Before going into the minutiae of these collections, the non-archaeological reader may be helped if we anticipate the chief conclusions: Eight-rowed flints, similar to those described above, were widespread in pre-Columbian times in the eastern United States. They go back to approximately 1000 A. D., and over wide areas in the *eastern* United States no other kind of

Fig. 4. A single ear of Stevens' Flint showing extensive husk-leaf development representative of many varieties of northern flint corn.

Fig. 5. Pachytene chromosomes of Longfellow Flint showing small organizer knob on chromosome 6. The largest arrow points directly to the organizer knob. It will be noted that the knob is so small as to be scarcely visible against the side of the nucleolus and is only slightly larger than the terminal chromomere of the satellite just below it. The smaller arrow points to the small terminal knob on chromosome 9.



Map 1. Distribution of collections of prehistoric corn in the eastern United States: large dots, crescent-seeded 8–10 rowed flints (i. e., like northeastern flints); small dots, various other types.

maize has been reported in archaeological remains. In the Great Plains, by contrast, there were widely divergent types of corn as well as northern flints and apparent mixtures with them. The sequence of these types of flint in the Great Plains remains to be worked out. The situation in the American Southwest is equally complex but one fact is certain: The northern flints arrived there relatively late (about 1300 A. D.), long after other types of maize had been established in that region.

The facts on which these conclusions are based are presented in condensed form in Table III and map 1. These summarize the collections of archaeological maize from the Great Plains and the eastern United States which we have so far examined, some 36 in all. They represent all the collections readily available at the Rochester Museum, the Peabody Museum of Harvard University, the Ohio State Museum at Columbus, the Museum of Ethnobotany of the University of Michigan, the National Museum at Washington, the Library of the Iowa State College at Ames, and the Chicago Museum of Natural History. To the curators and staffs of these museums we are greatly indebted. They not only made the material available for study but supplied us with literature and references in addition to much general information on archaeological matters. It will be noted that nothing from the southwestern states is included in this survey. The situation there is much too complex for discussion here and is somewhat outside the scope of this paper. For a detailed report on one prehistoric collection of southwestern maize

which includes 8-rowed flints, see Anderson's appendix to Haury's ('45) report on Painted Cave. For a general discussion of the evidence on types of maize in the Southwest see the fourth chapter, pp. 39-55, of Carter's ('45) "Plant Geography and Culture History in the American Southwest."

Some of the data in Table III are summarized in map 1. At least three main types of corn occur in the Northern Great Plains: (1) Varieties very similar, if not identical, to the northeastern flints described above. They have wide, crescent-shaped seeds, thicker at the apex of the kernel than near the germ. They are straight-rowed with strongly paired rows, and are predominantly 8-rowed. (2) In the Northern Great Plains, in addition to the above varieties, are others which are more or less similar but have higher row numbers and smaller, squarer kernels. (3) From rock shelters and caves from the Ozarks to southern Ohio are found collections of a very different type of corn. Some of these are well preserved. From others the evidence is fragmentary. They resemble the so-called prehistoric Basketmaker corn of the Southwest in their irregular-shaped kernels, their ears, which taper to the base as well as to the tip, and their high percentage of ears with row numbers from 12 to 14. Their presence in this area and their resemblance to Basketmaker corn raise questions which are completely outside the scope of this paper. The point in question is the 8-rowed crescent-seeded flints. Map 1 and Table III demonstrate that such varieties have been in the eastern and northern states for some centuries at least and that they were once very widespread there.

If we catalogue the varieties of corn by their general resemblance to each other in all characters rather than by the texture of their endosperm (Anderson and Cutler, '42) it will be seen that a number of sweet corns, a few of the older varieties of popcorns, and some of the flour corns of the eastern Indians are very closely related to the northeastern flints. They resemble them in their early maturity, crescent seeds, predominance of 8 rows, tillering, flag leaves on the ear, absence of prop-roots, and structure of the tassel. The few which we have examined are also very similar cytologically.

DISCUSSION

The northern flints as ancestors of modern corn-belt varieties.—

While the northern flints, as such, are now little more than a curiosity in much of the region where they were formerly grown, they are indirectly of both practical and theoretical significance because they are at least one of the ancestral types of the varieties which replaced them. There is abundant evidence that the varieties of the United States corn belt originated by repeated hybridization between the northern flints and soft-textured southern dents.

Until the early 1800's nothing like the big cylindrical, yellow maize of the corn belt, with its keystone-shaped, dented kernel, was known in the United States or elsewhere. As American agriculture developed and pushed westward the northern flints were progressively more and more mixed with soft white dents spreading up from the South. The latter were in many ways similar to some present-day Mexican varieties. Lorain, whose book appeared posthumously in

1825, described the ears of these southern dents as "not very long, neither is the cob so thick as that of the big white and yellow [flint]. But the formation of the grain makes the ears very thick. They frequently produce from thirty to thirty-two and sometimes thirty-six rows of very long narrow grains of a soft, open texture. These grains are almost flat, at their outside ends." He also states that this dent "ripens later than any other but is by far the most productive." (p. 203). The commonest name for these soft dents was "Gourdseed", since the flat kernels with a collapsed and more or less pointed tip resembled a pumpkin seed or gourd seed.

Lorain discussed in detail the results to be obtained from mixing Gourdseeds and flints and went on to say:

> "The quantity of the Gourdseed corn mixed with the flinty yellow corns, may be determined, so as to answer the farmer's purpose. When the proportion of the former greatly predominates, the grains are pale, very long and narrow, and the outside ends of them are so flat that but little of the indenture is seen. As the proportion of Gourdseed decreases in the mixture, the grains shorten and become wider, and their outside ends grow thicker. The indentures also become larger and rounder, until the harder corns get the ascendancy. After this the outside ends of the grains become thicker and more circular. They also grow wider, and the fluted appearance between the rows increases. The indentures also decrease in size until they disappear, and the yellow flinty varieties are formed. But as I believe, not so fully but that the latent remains of mixture will forever subject it to more or less change." (loc. cit., pp. 205–206).

The churning and rechurning of the Gourdseeds and the flints continued for several decades. By 1837, P. A. Brown listed seven different varieties known to him which had originated in that fashion. For the year 1850 we have an unusually complete picture. Before there was a Federal Department of Agriculture, the Patent Office published an annual summary of the progress of American agriculture; questionnaires were sent out to leading farmers and the replies were summarized and woven into an essay. For 1850 (U. S. Comm. Patents Rept., '50) the replies were printed practically as written, not even being sorted according to states. Since the first question to be answered had been: "What varieties of corn are most esteemed in your vicinity?", the replies give a detailed picture of the kinds of corn grown in the United States in the middle of the 19th century. The corn belt was just then taking shape in Ohio. Three of the replies from that state describe the mixing of flints and Gourdseeds which was taking place. "We cultivate several varieties of what is here called gourd-seed. They are all nearly a hybrid between the rough gourd-seed of the South and the flints of the North." (p. 371). Another letter asserts that the best varieties are "obtained by mixing the large Southern corn with that of the North." (p. 396). Another states that there are "many good varieties, mostly crosses between gourd-seed and the small flint." (p. 454). Only one reply about corn was received from Illinois which was then outside the corn belt (p. 245). It reports that in the vicinity of Quincy the most esteemed variety is "a species obtained by mixing the large yellow corn of Kentucky with the yellow flint." The white Gourdseed is also said to be planted. Mixtures of Gourdseed with various southern corns are specifically mentioned in reports from North and South Carolina, Virginia, Alabama, and Mississippi.

Northern flints alone are mentioned for Maine, New Hampshire, Connecticut and New York, and they were still among the outstanding varieties for Massachusetts, Ohio, Kentucky, Illinois and Michigan. The expression "dent corn", incidentally, is used only in the three letters from Michigan (pp. 309, 410, 412).

There can be little doubt then that our corn-belt dents originated during the first half of the nineteenth century by a manifold mixing of northern 8- and 10-rowed flints with many-rowed southern dents. In addition to the precise evidence given by Lorain and the Patent Office report for 1850 there are numerous references and descriptions in other agricultural writings. For detailed accounts the reader is referred to Edward Enfield's monograph on "Indian Corn," published in 1866; Fearing Burr Jr.'s, "Field and Garden Vegetables of America," 1863; Browne's, "Essay on Indian Corn" in The 'Farmers' Cabinet' for 1838, and the 'Transactions of the New York State Agricultural Society' for 1848.

The importance of northern flints in modern corn breeding.—

The demonstration that our corn-belt dents are derived in part from the northern flint corns is of more than academic interest. It has been shown (Anderson, '39) that in crosses where any considerable number of genes are concerned the total forces of varietal cohesion are vastly greater than is usually appreciated. In such crosses all the multiple-factor characters will be partially linked with one another, and while a bewildering variety of new forms may appear, on the whole, the combinations of characters which went into the cross together will tend very strongly to stay together in the hybrids. If the number of segregating genes exceeds three per average cross-over segment (a not unlikely figure in crosses between northern flints and southern dents) then the linkages can be broken only by long generations of controlled breeding. Though approximately a century has elapsed since the mixture of the southern dents and the northern flints was begun, we may well expect that enough of the genes contributed by the flint varieties are still so linked with one another, on the average, to render this linkage worthy of consideration in any corn-breeding program. In producing hybrid corn, for instance, some of the difficulties encountered are due to the fact that we are not working with a homogeneous mixture of dent corns as such; we are working with a mixture containing large blocks of germ-plasm of southern dents and of northern flints. Hard kernels, a low row number, cylindrical ears, and early maturity were qualities which went into corn-belt corn from the flints. It is a matter of common knowledge among experienced present-day corn breeders that these qualities still tend to stay together. Knowing that these qualities went in together from the flints, it should not take too long, by experimental breeding, to produce at least a rough estimate of their distribution in the germ-plasm of corn-belt varieties. Are they scattered equally over all ten chromosomes, or are they concentrated on a few? Are the gene differences to be estimated in the tens, the hundreds, or the thousands? It should be possible within a reasonable length of time to answer these questions in at least a provisional way, and data of this nature should be quite

useful to the modern corn breeder in his efforts to improve existing inbred lines and to create new and better ones.

Relationship between chromosome knob numbers and morphology of inbreds.—

There is as yet little exact evidence as to how completely the gene combinations introduced from the northern flints have been broken up in modern dent corns. Our determinations of chromosome knob numbers in 65 inbred lines of corn-belt maize bear directly on this point (fig. 3).

While the numbers of inbreds investigated is still too small to represent an unequivocal demonstration, the general trend in ear and plant morphology from one extreme to the other as one passes from inbreds with low knob numbers to those with higher numbers is most suggestive. The inbreds with knob numbers of approximately two are clearly the most like the northern flints of any of the 65 which have been studied. It would seem that the total effect of the forces holding the germ-plasm of the northern flints together is so strong in modern maize, even after a century of mixing, that the coherence can be demonstrated cytologically. If this be true, it represents racial coherence of a very high order of magnitude, for the knobs serve as cytological markers for only a portion of the germ-plasm. Any specific knob can serve only as a marker for the arm or part of arm of the particular chromosome in which it occurs. Since there are 10 chromosomes and therefore 20 chromosome arms, the difference between the high knob lines of 8 and the low knob lines of 2 is at most a difference in only 6 out of the 20 arms, or 30 per cent. It seems, therefore, significant that with markers in only 30 per cent of the chromosome arms, there is still an indication of resemblance to the northern flints in the low knob inbreds.

It may be that when a larger number of inbreds have been examined the relationship between low knob numbers and flint-like characters will not be as definite as these preliminary results have indicated. The low knob number of the northern flints, however, is definitely established. This fact poses a number of questions since it seems to be in direct opposition to Mangelsdorf and Cameron's ('42) pioneer work on the same subject.

Mangelsdorf and Cameron determined the knob numbers of over 150 varieties of maize from Guatemala and demonstrated the association of high and of low numbers with various contrasting characters of the ear and plant. Two of the most definite associations which they established were between high knob number and cylindrical *vs.* tapered ears, and with straight rows *vs.* irregular rowing. On the basis of their findings we might expect the northern flints to have the highest knob numbers of any United States varieties of corn. Actually they have the lowest, as we have shown above. These two facts, however, are not as diametrically opposed as they might seem. The corn of the United States is not the corn of Guatemala, nor could all of it have been directly derived therefrom. Much of it, theoretically the greater part of it, must have spread into the United States by way of Mexico. For that country we have only about 50 knob determinations but in

general they agree with those of Mangelsdorf and Cameron. In western Mexico there is a whole group of varieties with cylindrical ears, high-lodging resistance, and growing chiefly at low altitudes. They have high knob numbers as Mangelsdorf and Cameron would predict. In Central Mexico, mostly at very high altitudes, there is a group of tapering-eared dent corns which lodge badly and are smut-susceptible. Mangelsdorf and Cameron would predict them to have generally low knob numbers which they do, being from 0 to 5 in the material we have investigated. Much of the dent corn of Mexico is intermediate between these two extreme types (Anderson, '46), and the few examples we have investigated have intermediate knob numbers as might be expected. It was such varieties as these which eventually spread northward into the United States. If for the moment we sidestep the question of where the northern flints came from originally but keep in mind that they have few or no knobs, then our results come closer to falling into line with those of Mangelsdorf and Cameron. By a mixture of old, southern dents with mediumly high knob numbers and northern flints with few knobs or none, then a situation such as we have described would have developed.

Origin of the northern flints.—

The above hypothesis is satisfactory as far as it goes, but it leaves unexplained the origin of the northern flints and advances no reasons for their having few or no knobs. Only the most tentative of explanations can be offered at the present time. As has been pointed out above, the northern flints are characterized by wide, crescent-shaped seeds on a cylindrical, few-rowed ear with a strong cob more or less enlarged at the base and borne on a stout shank. This is a distinctive combination of characters. Since somewhat similar varieties are known in the American Southwest, Mangelsdorf and Reeves originally suggested ('39) that the northern flints spread into the eastern United States from that direction. In this respect they are almost certainly wrong. We have specific archaeological evidence that the northern flints are definitely pre-Iroquoian in eastern North America (see pl. 6). There is abundant and definite evidence (Carter, '45; Carter and Anderson, '45) that varieties like the northern flints did not reach the American Southwest until after 1200 A. D. There is even some evidence to suggest that they reached the Southwest as varieties relatively similar to those in the East and that they then underwent hybridization with some of the varieties already present in the Southwest to produce the typical long-eared sorts of the modern pueblos (Haury, '45). Furthermore, the very similar long-eared varieties of northern Chihuahua most certainly represent relatively late southern extension *into* Mexico as had already been determined from cultural evidence (Sayles, '36).

If the northern flints could not have spread from the Southwest, whence could they have come? Varieties with wide kernels, stout cobs, and a more or less enlarged base are practically unknown from most of Mexico. However, they are present in Guatemala and adjacent Chiapas. It seems probable that northern flint corns may be among various cultural traits which spread from south of the

Isthmus of Tehuantepec into the eastern United States without leaving any very clear record of the route by which they journeyed.

If the northern flints did come from Guatemala, it is still necessary to explain their low knob number, since many of their ear and plant characters are essentially those Mangelsdorf and Cameron ('42) found to be correlated with high knob number in their Guatemalan survey. They interpreted the high knob number as due to crossing with teosinte, which is known to have a very high knob number and which, according to Mangelsdorf and Reeves' hypothesis ('39), was itself derived from previous hybridization between maize and *Tripsacum*. On these hypotheses, therefore, the high knob numbers and the associated characters came ultimately from *Tripsacum*, and Mangelsdorf and Cameron applied the term "tripsacoid" to these varieties. Since that time, however, Graner and Addison ('44) have reported that *Tripsacum australe* of South America, unlike its North American relatives, is lacking in terminal knobs. Assuming that Graner and Addison's observations are typical of the cytological picture in *Tripsacum australe*, then we are faced with the possibility that introgression of *Tripsacum* germ-plasm into *Zea* might have various effects upon knob number, as Cutler ('46) has recently suggested. It is quite possible, therefore, that our results with the northern flints can be harmonized with the hypotheses put forward by Mangelsdorf and his collaborators. Before that can be accomplished, however, we shall need to have a much more detailed understanding than we have at present of the relationships between the northern flints and similar varieties in Central and South America.

SUMMARY

1. Though no longer of much commercial importance, the northern flints are of interest to anthropologists as a type of corn once very wide-spread in the eastern United States. They are also worthy of consideration by modern corn-breeders as one of the ancestors of modern United States dent corns.

2. A representative collection of northern flint varieties was grown. Its gross morphology, its pachytene cytology, were systematically investigated. The varieties of flint corn from New York and New England are substantially uniform morphologically, cytologically and archaeologically. Similar varieties are also grown on the Northern Great Plains, but the collection from that area is more variable and includes other types, as it has since prehistoric times.

3. The northeastern flints (those from New York and New England) have slender culms, irregular tillers, well-developed flag leaves, few visible prop-roots, and are of early maturity. Their ears are cylindrical, 8- to 10-rowed, with strong shanks and proportionately large cobs. Their kernels are wide, undented, and not pointed. The tassels are wiry, with no condensation. The central spike bears its spikelets in whorls of two pairs: the pairs 4-ranked and decussately arranged on the spike.

4. The pachytene chromosomes of the northeastern flints show few knobs or none at all, and the knobs, when present, are usually small.

5. There is abundant archaeological evidence to show that similar varieties of corn were common in eastern North America in prehistoric and protohistoric time. Over wide areas in the eastern states they are the only maize so far obtained in archaeological excavations.

6. The northeastern flints were widely grown commercially in the United States in colonial times and afterward. During the first half of the 19th century they were extensively and repeatedly hybridized with soft dent varieties from the South, giving rise eventually to the typical cylindrical-eared dent varieties of the United States corn belt.

7. Though the amalgamation of the northeastern flints and the southern dents has proceeded for nearly a century, some of the characteristics of the northern flints are still more or less linked in the germ-plasm of modern United States commercial corns. A cytological survey of 65 inbred lines of dent corn showed chromosome knob numbers of from 2 to 8. The inbreds with the lowest knob numbers (i.e. the most flint-like) were most similar to the flints in their external morphology.

8. The origin of the northeastern flints is briefly discussed. While they are, in general, unlike Mexican maize but show strong resemblances to certain varieties from Guatemala, the problem cannot be seriously approached until more detailed information concerning the morphology and cytology of Central and South American varieties is available.

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Explanation of Plates 1–5

In these plates the lance-shaped object at the left-hand margin is a tracing of the first leaf above the ear. In the photographs of the ears each of the divisions on the scale represents one centimeter.

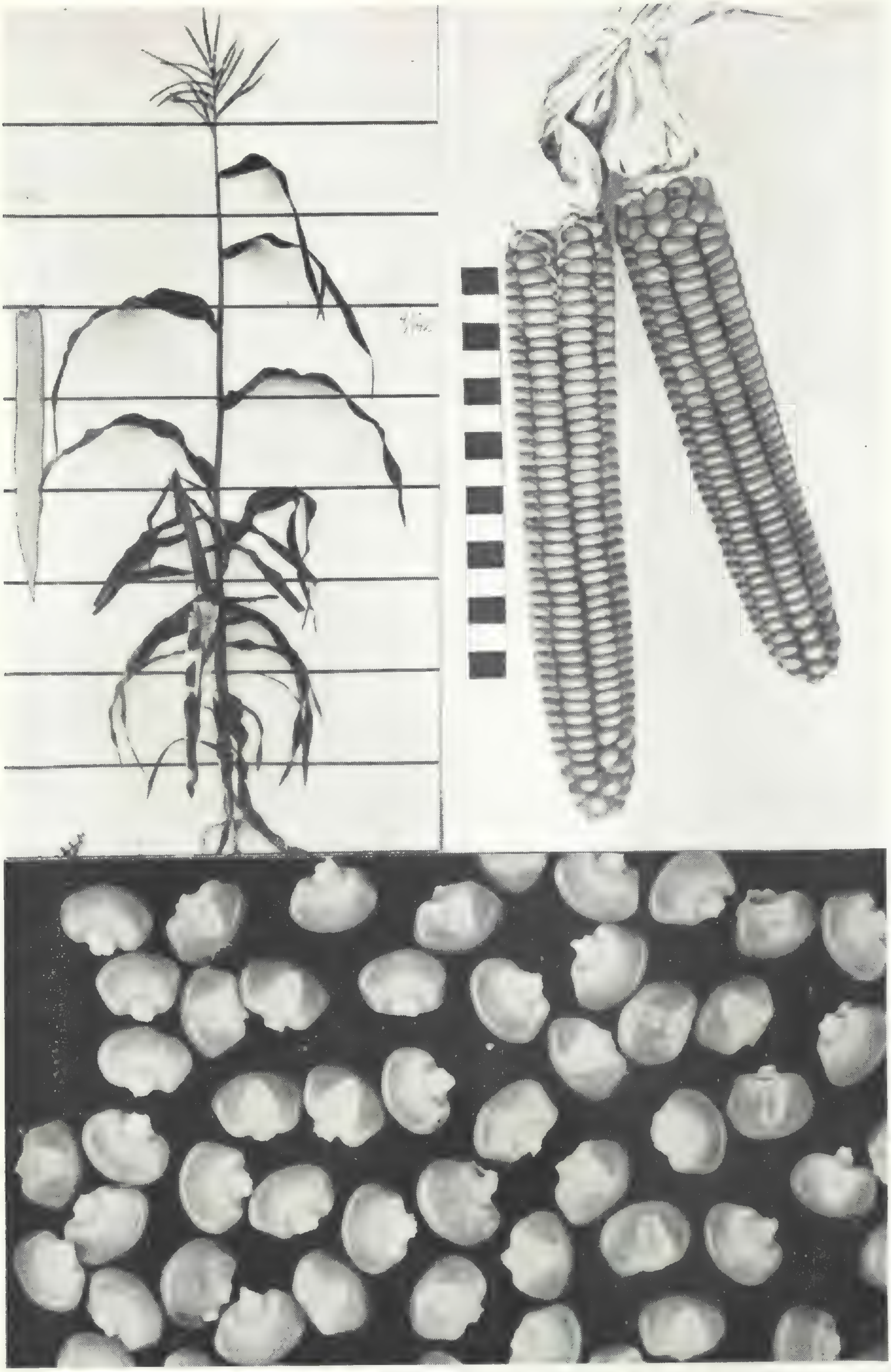
Plate 1. Stevens' Flint—typical plant, ears, and kernels.

Plate 2. Parker's Flint—typical plant, ears, and kernels.

Plate 3. Dakota White, a variety of the Great Plains having many characteristics of eastern flints.

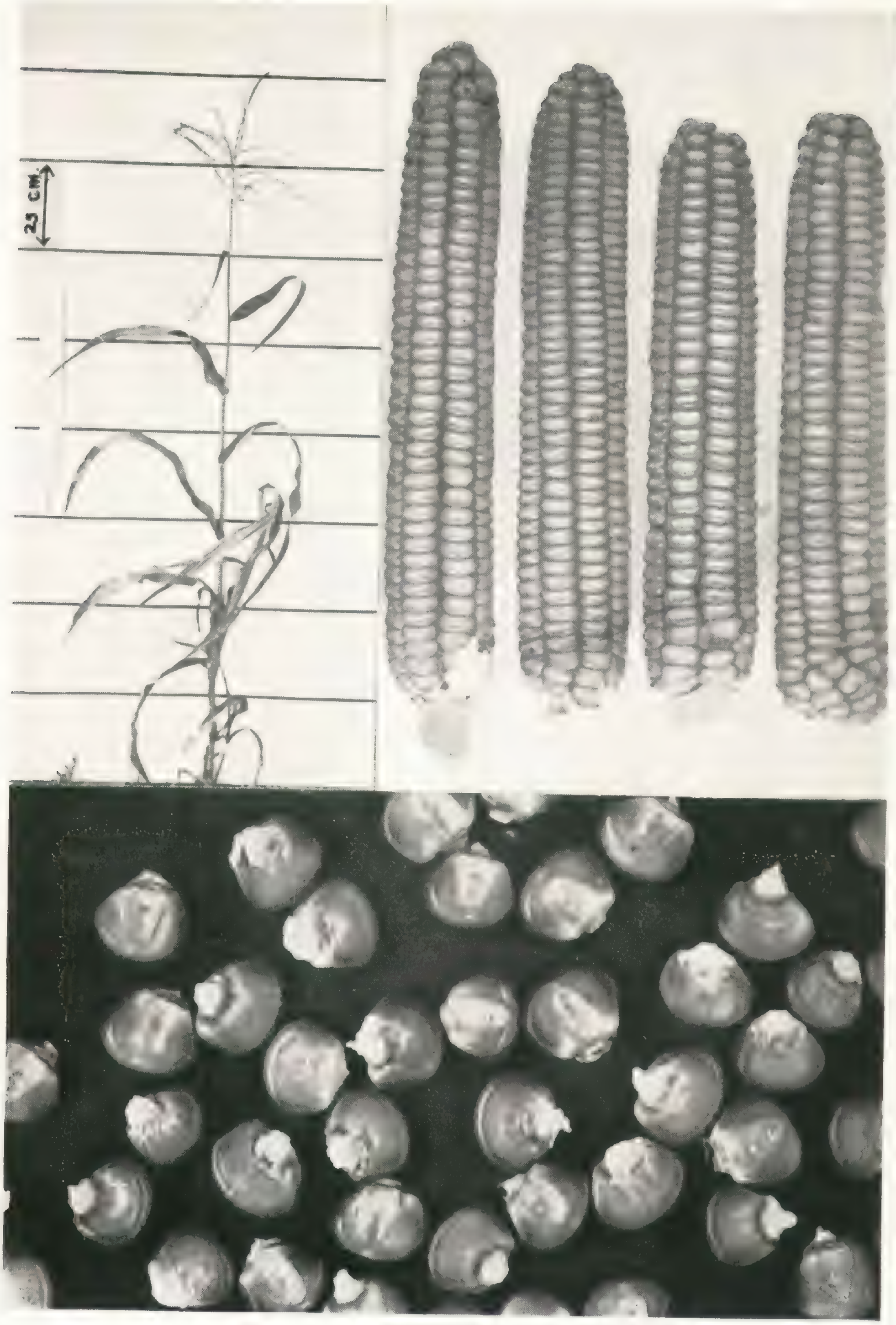
Plate 4. Twelve-row Dakota. This type is quite different morphologically from the northeastern flints but similar in many ways to certain varieties of the southwestern states.

Plate 5. Spanish Popcorn. Representative plant, ears, and kernels. A flint of very early maturity whose morphology suggests relationship to both northeastern and Great Plains varieties.



STEVENS' FLINT

BROWN & ANDERSON—NORTHERN FLINT CORNS



PARKER'S FLINT

BROWN & ANDERSON—NORTHERN FLINT CORNS

DAKOTA WHITE

BROWN & ANDERSON—NORTHERN FLINT CORNS

TWELVE-ROW DAKOTA

BROWN & ANDERSON—NORTHERN FLINT CORNS

SPANISH POPCORN

BROWN & ANDERSON—NORTHERN FLINT CORNS

Explanation of Plate

PLATE 6

Photographs of charred maize cobs from Gibraltar Site, Wayne Co., Mich., collected by Dr. Emerson F. Greenman, Museum of Anthropology, University of Michigan, summer 1938. "Owasco" (probably before 1200 A. D.). Note the 8-rowed cobs, the wide alveoli, strongly paired rows, and large shanks. Photograph courtesy of Volney Jones and the Museum of Ethnobotany of the University of Michigan.

BROWN & ANDERSON—NORTHERN FLINT CORNS

MYCOCANDIDA RIBOFLAVINA

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Professor in the Henry Shaw School of Botany of Washington University

The following study is based on culture no. 921, resulting from a long series of selections from stock culture no. 321 in the collection of Anheuser-Busch, Inc., St. Louis. The latter was originally isolated from figs by H. J. Phaff and sent under the name *Saccharomyces fragilis* ?.[1]

Mycocandida riboflavina Dodge, sp. nov.

Pseudomycelium ex cellulis longe ellipsoideis, 10–11 × 1.6–2.5μ, ramis lateralibus 1–2(–4) ad quemque nodum, cellulis 1–3. Colonia parva, cremea vel albida, laevis vel subfoveolata, margine tenui. Colonia rugosa cremea, crateriformis, rugis radiantibus, subelevatis, margine crassiori. Gelatina tarde liquefacta. Glucosa, fructosa, mannosa, sucrosaque fermentatae.

Cells in young cultures variable in shape from ellipsoid to long-ellipsoid, or ovoid, often with both ends rather acute, budding polar, but cells not apiculate as in *Kloeckera (Pseudosaccharomyces)*, mostly single, a few in short chains.

In old liquid cultures (four months) similar to young cultures but chains somewhat longer with 2 (rarely up to 4) short branches at the nodes (up to 3 cells long), cells ellipsoidal to subpyriform, terminal cells short-ellipsoid to nearly spherical; one spherical cell seen with 4 buds at one end and 3 at the other.

On old malt agar cultures, pseudomycelium well developed, cells 10–11 × 1.6–2.5μ, branching lateral, only 1 or 2 branches at a node, cells long-ellipsoid or with the end bearing the branch slightly enlarged and more rounded; terminal cells shorter.

No ascospores produced on old cultures (some completely dried out) nor on gypsum blocks nor on Gorodkova agar.

COLONY CHARACTERS AND SECTORING

On malt extract agar (15° Balling), colony small, margin thin, sloping gently to the center, surface smooth with very minute pitting and with some very shallow radial valleys, with a small rugose sector. Transfers from the rugose sector produced colonies with a shallow central crater, with low broad radial folds and a few cross folds, margin circular and somewhat elevated, with a smooth sector occupying about one-sixth the circle. Colonies cream buff with a lighter margin. Transfers from the smooth sector produced colonies with a very low dome in the central crater, sloping gently to the margin, with 4 or 5 radial valleys, surface smooth with some very shallow pits (visible under a 9 × hand-lens), margin very smooth and slightly elevated. Colonies cartridge buff or darker, margins somewhat lighter. No further sectoring occurred on smooth colonies.

[1] Mrak, E. M., H. J. Phaff, R. H. Vaughn, and H. N. Hansen. Yeasts occurring in souring figs. Jour. Bact. 44:441–450. 1942.

Issued March 29, 1947.

On Sabouraud glucose agar, colonies with a low central plateau, broadly crenate margins with narrow radial valleys connecting the central plateau to the notches in the margin. Transfers from the smooth type of colony on malt extract agar produced colonies with a nearly smooth center (only a very faint suggestion of a crater), sloping very gently to the margin, surface rather dull from minute pitting (about the limits of visibility with a 9 × hand-lens), no radial valleys nor ridges, margin less elevated, with the faintest suggestion of marginal striation (under 9 X lens). Color pale ochraceous salmon. Transfers from the rugose sector on malt extract produced colonies with a low central dome in a very shallow excentric crater, sloping gently to the margin, a very few slight ridges and radial valleys (arranged as the lamellae of a mushroom). Colony light ochraceous salmon, margin paler. No sectoring was observed on Sabouraud glucose agar.

Yeast decoction agar: colony more elevated, very moist and shining, faint depression in center with about 4 very shallow, radial valleys, pure white. Transfers from either smooth or rough sectors on malt extract agar produced the same type of colony on yeast decoction agar.

BIOCHEMICAL ACTIVITY

In general, liquid cultures produced a slight ring on the sides of the tube, no islets nor pellicle; the liquid remained clear and the sediment finely granular; in old liquid cultures (about 4 months), the ring is a little better developed and the sediment becomes slightly more flocculent. In fermentation tubes of glucose, mannose and lactose, a few islets developed but they were never abundant nor did they coalesce to form a pellicle. Litmus milk was neither acidified nor coagulated; a slight ring and abundant sediment developed in the tubes, showing that growth occurred. Gelatin was very slowly liquefied, complete in 16 weeks, abundant sediment, but no ring nor pellicle.

Fermentation: Gas is produced with glucose, fructose, mannose and sucrose, none with maltose nor lactose. Gas is produced much more slowly than with *Saccharomyces cerevisiae*, not showing until the second day after inoculation. No acid was produced under anaerobic conditions (long arm of fermentation tube); acid with glucose and lactose, none with mannose, maltose nor sucrose under aerobic conditions (short arm of fermentation tube). Sediment abundant in all tubes.

Since our organism was thought possibly related to *Brettanomyces* and since most species of the latter produce an after-fermentation of beer, 95 per cent ethyl alcohol was added to 15° Balling malt extract to make final concentrations of 5–12 per cent ethyl alcohol. At 5 per cent after three weeks, there was good growth with abundant flocculent sediment; at 6 per cent growth was good, but with less and more granular sediment; at 7 per cent growth was poor with very fine granular sediment. No growth at 8–12 per cent, hence the limiting concentration of alcohol lies between 7 and 8 per cent ethyl alcohol.

Two hundred ml. portions of Budweiser beer (4 per cent alcohol) were measured into flasks under aseptic conditions, and one set inoculated with *Myco-*

candida riboflavina, the rest being reserved as a control. The flasks were weighed daily. In 6 weeks, 2 gm. loss of weight was recorded, with a decrease of alcohol to 1.1 per cent (volume) and an increase in non-volatile organic acids measured. Had the organism been a species of *Brettanomyces*, an increase in ethyl alcohol and volatile organic acids would have been obtained.

TEMPERATURE RELATIONS

Week-old cultures in malt extract (15° Balling) were placed in a water bath at the desired temperature for half-hour and hour intervals. Good growth on subsequent plating occurred at 48° C. for a half hour and at all lower temperatures. No growth occurred at 49° C. nor above to 58° C. after half-hour exposures. About 20 colonies per plate were found on plates from cultures exposed to 48° for one hour; hence we conclude that the thermal death point is 49° for a half-hour exposure, and the maximum temperature for growth is 47–48° C. While no extensive experiments were made to determine optimum temperature for growth, such experience as we have had indicates that the optimum is about 30° C.

RELATIONSHIPS

At first examination of young cultures, our organism might be taken for *Kloeckera (Pseudosaccharomyces)*, as the cells are rather elongate with acute ends, but not truly apiculate. Little or no pseudomycelium has ever been reported in *Kloeckera*, while our organism predominantly produces pseudomycelium in old cultures, placing it in the Eremascaceae Imperfectae. *Brettanomyces*, when grown on potato agar, resembles our organism in morphology, but fails to liquefy gelatin, produces sufficient volatile acid in malt extract to kill the cultures quickly (unless calcium carbonate is added to the medium), and ferments sugars very slowly. Our organism liquefies gelatin slowly, produces no volatile acid under similar conditions, and ferments sugars more rapidly if they be fermented at all.

Both morphologically and physiologically, our organism belongs in *Mycocandida* Langeron & Talice[1], based on the type species *Candida mortifera* Redaelli[2]. Our organism differs from the type species in its fine granular sediment rather than flocculent growth with little sediment, liquefying gelatin more slowly and fermenting fewer sugars but growing better in those it does not ferment. Our organism has longer, slenderer ellipsoidal cells in malt and other media, while *M. mortifera* has nearly spherical ellipsoid cells.

Our organism resembles *Candida Guilliermondi* (Cast.) Langeron & Guerra[3] in its fermentative ability, but the latter forms a pellicle on liquid media, fails to liquefy gelatin, renders litmus milk alkaline, fails to assimilate lactose, and has larger cells and pseudomycelium. Although some strains approach the morphology

[1] Langeron, M., et Talice, R. V. Nouvelles méthodes d'étude et essai de classification des champignons levuriformes. Ann. Parasitol. Hum. Comp. **10**:1–80. *5 pls.* 1932.

[2] Redaelli, P. I miceti come associazione microbica nella tuberculosi polmonare cavitaria. Osservazioni micopatologiche e sperimentali. pp. 21–24. Pavia, 1925.

[3] Langeron, M., et P. Guerra. Nouvelles recherches de zymologie médicale. Ann. Parasitol. Hum. Comp. **16**:429–476. *pl. 12–24.* 1938.

of *Mycocandida* on some media, in general it has the type of pseudomycelium of *Syringospora (Mycotorula)*.

Our organism differs from strain 488 (isolated by L. J. Wickersham from sour milk and used by P. R. Burkholder[4] in patent 2,363,227 under the name *Candida Guilliermondia*) in producing as good growth in lactose as in mannose and sucrose. *Candida Guilliermondi* (Cast.) Lang. & Guerra produced no growth on lactose and maltose while *C. Guilliermondia* Burkholder produced better growth on maltose than on glucose and only slight growth on lactose.

Our organism was thought to be an aberrant strain of *Saccharomyces fragilis* when first isolated and might be considered an asporogenous variant. It has the same general morphology when first transferred to fresh media, but is smaller, the cell walls are not fragile, and it has produced no ascospores by the usual techniques. It liquefies gelatin much more slowly and fails to ferment lactose. I have found no report of *S. fragilis* producing pseudomycelium in old cultures.

In view of the above considerations, our organism is an undescribed species of the Eremascaceae Imperfectae for which I propose the name *Mycocandida riboflavina*.

In conclusion, I wish to express appreciation to Anheuser-Busch for a research grant and permission to study this organism; to Dr. George W. Freiberg for helpful suggestions and photostats of pertinent literature not available in local libraries; to Dr. J. E. McClary for determinations of ethyl alcohol and volatile and non-volatile acids; to Dr. Lilian Nagel for the drawings illustrating morphology; and to Dean George T. Moore, of the Henry Shaw School of Botany of Washington University, for kindly interest in this study.

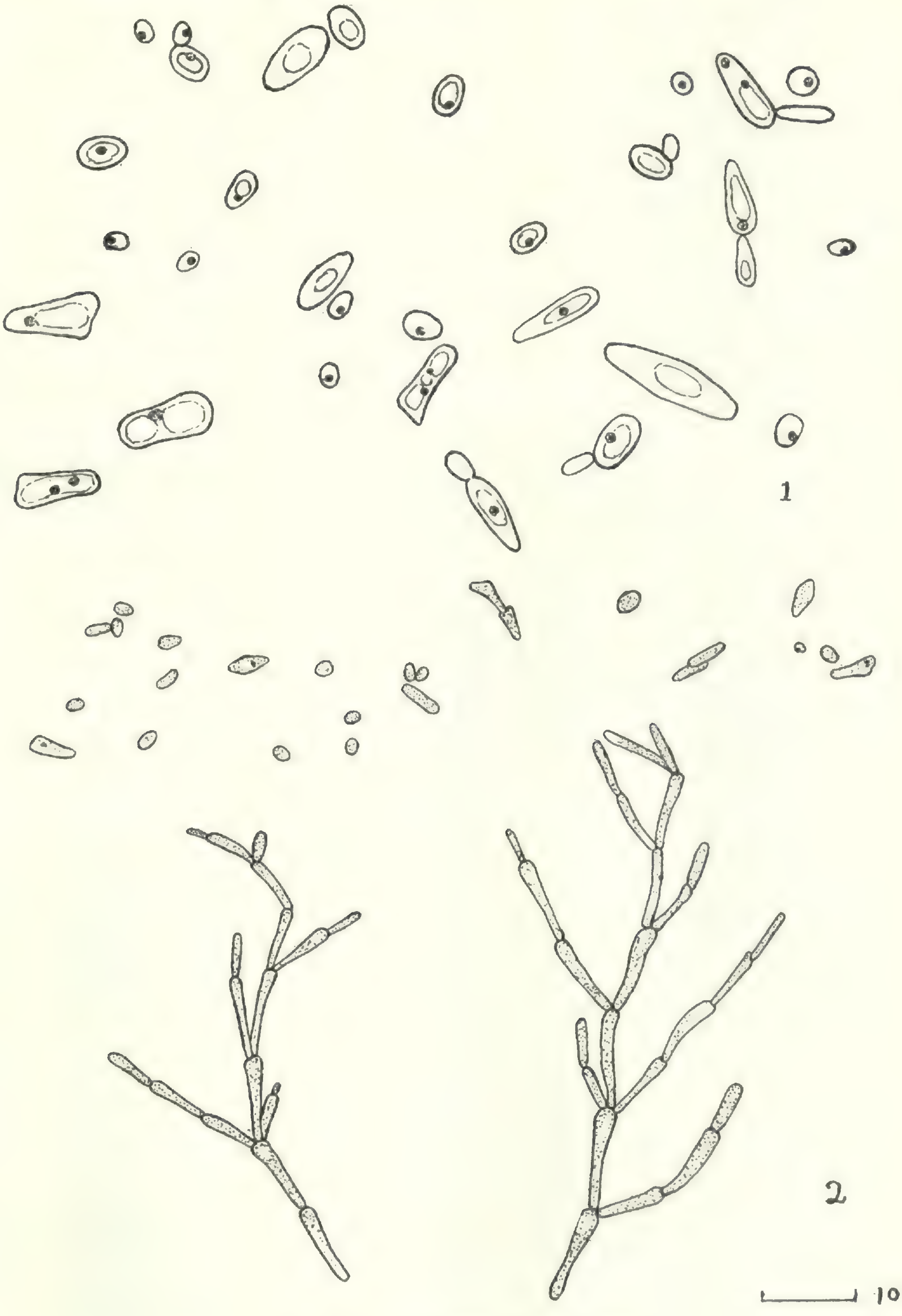
[4]Burkholder, P. R. Fermentation process for the production of riboflavin (vitamin B_2). U. S. Patent Office 2,363,227:1–3. 1944.

Explanation of Plate

PLATE 7

Fig. 1. Cells from 3-day agar culture at room temperature.

Fig. 2. Cells from dried-out colony on agar plate, soaked in distilled water and stained with aceto-orcein. 10 × ocular, 90 × objective.



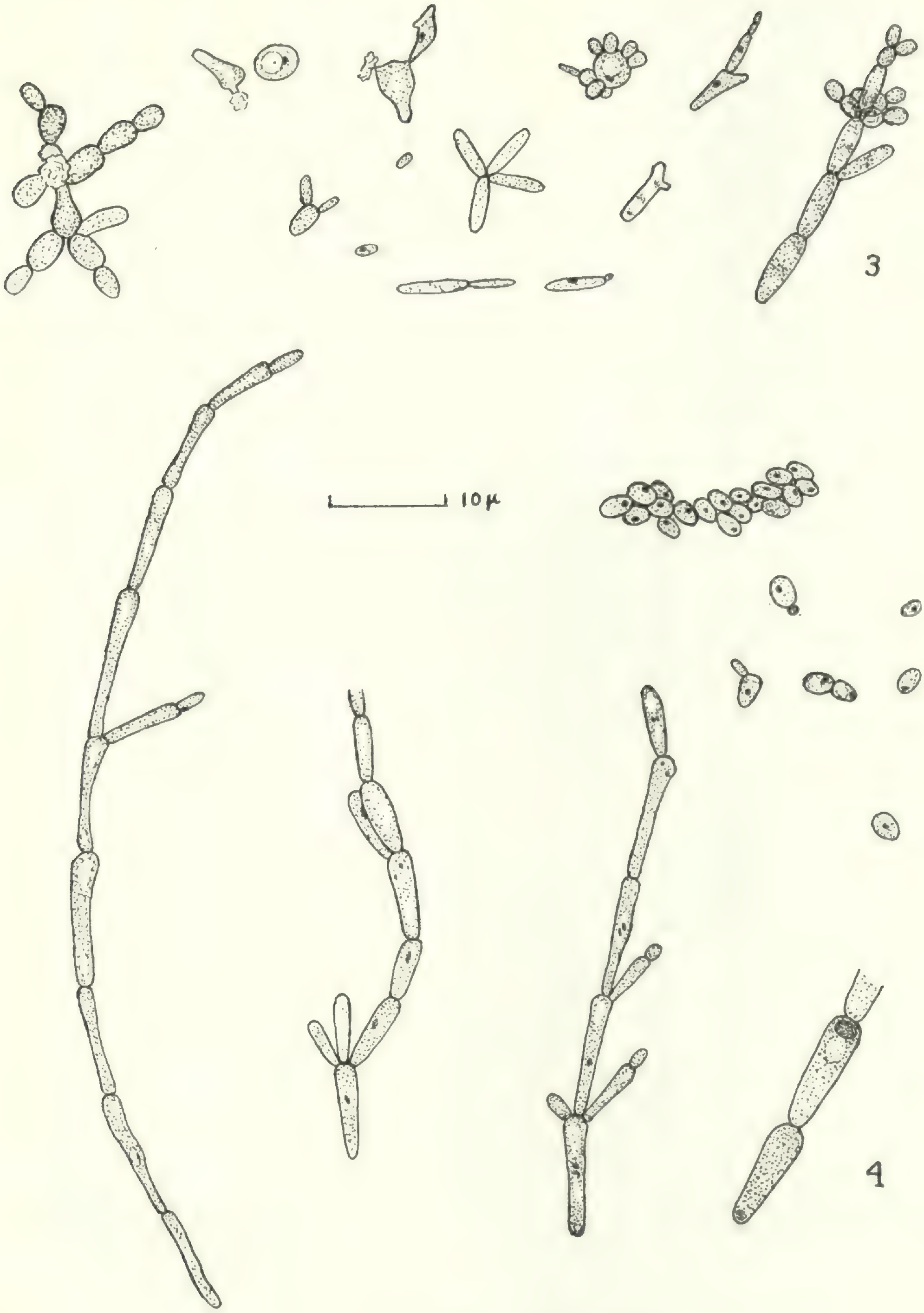
DODGE—MYCOCANDIDA RIBOFLAVINA

Explanation of Plate

PLATE 8

Fig. 3. Unusual types of cells from old lactose fermentation tube. Free-hand sketches.

Fig. 4. Pseudomycelium and cells from moist colony on agar slant, stained with aceto-orcein. 10 × ocular, 90 × objective.



DODGE—MYCOCANDIDA RIBOFLAVINA

INHERITANCE IN THE CARNATION (*DIANTHUS CARYOPHYLLUS*)
III. Inheritance of Flower Color

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Introduction

This carnation study was begun by the senior author in 1932 at the University of Connecticut, and although only about 3,500 plants were grown there, that represented much of the work necessary before larger populations could profitably be grown.[1] In 1936 the study was transferred to the University of California where, between 1936 and 1942, 35,000 to 40,000 plants were grown. Since 1946 the work has been continued at the Missouri Botanical Garden.

The purpose of this study was partly to produce superior carnation varieties; especially in the yellow group where good commercial varieties have always been scarce, and partly to learn the genetical basis for some of the characteristics which contribute to the make-up of a good commercial variety. As the project expanded it was found necessary to limit the study to one or two major characteristics. Since a pleasing flower color is one of the primary requirements of any plant grown for ornamental purposes, this feature was gradually given preference, while others were given attention only as they appeared in the cultures grown for color analysis. Although the study is by no means complete, it seems justifiable to report the data obtained to date, as it may be some time before the work, interrupted by the war, can be resumed on full scale.

Material and Methods

The carnation material available during the first season consisted of ten commercial varieties, or clones, namely: ARCTIC, BETTY LOU, FAIRY QUEEN, IVORY, MAINE SUNSHINE, MATCHLESS, PINK ABUNDANCE, SPECTRUM, SURPRISE, and WOBURN. A few others were added during the next two years. Since carnation varieties of this type are ordinarily reproduced by cuttings, they were expected to be rather highly heterozygous. In order to get an idea of the degree of heterozygosity and at the same time make a start toward the production of relatively pure lines, self-pollination of these varieties was immediately undertaken. However, one variety (PINK ABUNDANCE) produced no pollen whatever during the entire season, and two varieties (SPECTRUM and IVORY) failed to set any seed whether self-pollinated or cross-pollinated. On the whole, selfing proved to be difficult and produced relatively few viable seeds per capsule. Crosses, on the

[1]The senior author is indebted to Professors R. H. Patch, G. S. Torrey, A. S. Porter, and S. P. Hollister for their kind interest in the project while it was carried on at the University of Connecticut. It was through their combined efforts that the necessary facilities were provided.

other hand, resulted in fair amounts of good seed and were easily made. Those varieties which produced little or no pollen proved to be among the best seed-producers when cross-pollinated. In the generations following these crosses many plants were eventually obtained that were reasonably self-fertile and could be inbred until relatively pure lines were established. Whenever a line of twenty-four or more seedlings failed to show any segregation for the characteristic being studied, the line was considered homozygous for the corresponding gene. This number is obtained by solving the equation $1-(3/4)^n = .999$, where n is the number of self seedlings that must be grown from a plant to indicate with a probability of .999 whether a plant that does not segregate is homozygous for the genes under investigation.

It was later found that varieties which could not ordinarily be selfed during the winter in the greenhouse, either due to lack of pollen or because of failure to set seeds, could be selfed with at least a fair amount of success if they were grown in the field during the summer and in the fall transferred to rather small pots and placed in the greenhouse. Even varieties which when benched, as is ordinarily done with this type of carnation, produced no pollen, with pot culture produced at least a few anthers and set good seeds. If the nitrate level was kept fairly low and the plants held rather on the dry side, this partial fertility often lasted well into the winter.

The seed was germinated in the greenhouse, the bulk of it in sterilized sand or soil. The seeds of the most important lines, and those which for some reason were poorly developed, were germinated on blotters and transferred to soil shortly after germination. Regardless of which method was used, most of the seedlings were transferred to 2-inch pots or 2-inch plant bands and later planted out in the field. A few were transferred to 4-inch pots and flowered in the greenhouse. Whether grown in the greenhouse or in the field, the progenies from crosses generally bloomed in from five to eight months whereas those from selfed lines were decidedly more irregular, requiring from five to fifteen months from planting of seed to flowering.

The chromosome number was determined from root-tip material on over 100 different plants. The $2n$ number was 30 except for occasional tetraploid root tips or sectors. Meiosis has been studied only in some 30 plants, all of which showed 15 bivalents at *IM*. Included in these 30 were 4 female sterile, 4 male sterile and 3 which ordinarily failed to produce seeds because of the prevalence of secondary ovaries. All underwent regular meiosis. $n = 15$ is the x number for the genus *Dianthus* (Darlington, '45). All observations are based on permanent preparations that were stained according to Stockwell's safranin-crystal violet schedule (Stockwell, '34).

In recording flower color, the names used in commercial carnation culture were retained; but new colors were given descriptive names.

Results

To facilitate the analysis, the colors of the carnation have been divided into four main groups, namely:

I. The *acyanic* group, containing only those colors that are due to anthoxanthins[2]. These colors are pale yellow, clear sulphur-yellow and white.

II. The *cyanic* group, in which the colors are due to anthocyanins on ivory base. This group contains two distinct series depending on whether the anthocyanin involved is pelargonidin or cyanidin. Each of these series may again be divided into two sub-series depending on whether the anthocyanin occurs as a monoglycoside or as a diglycoside.

a. Pelargonidin monoglycoside colors: salmon (ELEANOR, CHARM); red (SPECTRUM, KING CARDINAL, TOM KNIPE, WM. SIM).

aa. Pelargonidin diglycoside colors: light pink (VIRGINIA); deep pink (PINK ABUNDANCE, BOSTON WARD, JOHN BRIRY).

b. Cyanidin monoglycoside colors: lavender-pink (no commercial); crimson (WOBURN, TOPSY, SETH PARKER).

bb. Cyanidin diglycoside colors: lavender-pink (no commercial); purple (ROYAL PURPLE, POTENTATE).

III. The *transition* group in which the color is due to partial development of anthocyanin on yellow base. This group contains the salmon-yellow, orange, salmon-orange and pale maroons. Some of these self colors may be variegated with anthocyanin, in which case they are specifically discussed in the next group.

IV. The *variegated* group containing all those types in which either acyanic or cyanic colors occur in stripes or zones on lighter background. Five types of variegations will be discussed as follows:

a. *random narrow.*

b. *random broad.*

c. *picotee pattern.*

d. *salmon-red.*

The fifth type of variegation, *flushed*, because of its more natural relationship to the self colors, will be discussed in connection with the acyanic group.

I. The Acyanic Group

a. Yellow versus White.—

Most of the F_1 progenies from crosses between white and yellow have been either pure white or white lightly striped with anthocyanin color, but some have been anthocyanin self-colored. In Table I are summarized the results from those in which the F_1 were white or white-variegated. As variegation is discussed separately, only the self colors are considered here. The results indicate that two independent genes govern development of the yellow and white colors respectively,

[2] "Anthoxanthin" is a rather general term applied to sap-pigments other than those of the anthocyanin type. It refers in most cases to flavone derivatives.

TABLE I

PARENTAGE	GENERATION	PROGENY				TOTAL	RATIO	P
		White var. pink	White	Yellow	Pale Yellow			
MAINE SUNSHINE*, yellow	P_1			63	15	68	3:1	.20
34006-2, yellow	P_1			17	7	24	3:1	
34518-1-14*, yellow	P_1			24		24		
38192-14, yellow	P_1			27		27		
38168-1, pale yellow	P_1				21	21		
37054-6, white	P_1					**		
37079-29, white	P_1		30			30		
37109-1, white	P_1		23			23		
38594 = 34518-1-14 x 37054-6	F_1	30				30		
Two plants	F_2	95	85	41	12	233	12:3:1***	.65
38626 = 34006-2 x 37109-1	F_1	13	14			27	1:1	
Two pl., white var. D. P.	F_2	48	30	19	6	103	12:3:1	.95
One plant, white	F_2		66	20	5	91	12:3:1	.75
38628 = M. S. x 37109-1	F_1	9	5			14		
One plant, white	F_2		61	24		85	3:1	.45
One plant, white	F_2		42		11	53	3:1	.45
40522 = 38192-14 x 37109-1	F_1	27	18			45	1:1	
Three pl. white var. D. P.	F_2	69	94	38	12	213	12:3:1	.85
40576 = 38168-1 x 37079-29	F_1		26			26		
One plant	F_2		17		7	24	3:1	

* MAINE SUNSHINE at times had occasional broad, white stripes and faint, narrow pink stripes; 34518-1-14 had faint narrow reddish stripes.

** 37054-6 was female sterile, hence no P_1 population.

*** The white and white variegated pink have been added.

and that the gene for white is epistatic to the one for yellow. Because the so-called whites are really ivory-colored, at least in the bud stage or until bleached in sunlight, the gene controlling the development of this color has been designated *I*. The gene for full yellow color has been designated *Y*. Thus *YI* and *yI* are white, *Y i* yellow and *y i* pale yellow.

The whites used as parents in the crosses summarized in Table I, with one exception, were pure ivory-white on which no red or pink marks had ever been observed. The one exception, 37079-29, in the greenhouse during the short days of winter at times had a faint tinge of pink. Under field conditions it had pure white petals with tinted anthers. The four yellow parents, on the other hand, regularly produced a few reddish or pinkish stripes. Some of the yellow F_2 plants also had some reddish or pinkish stripes but in the field they were so indistinct that no accurate scoring could be made for this feature. The crosses in which the F_1 progenies were anthocyanin-colored are summarized in Table IV.

TABLE II

PARENTAGE	GENERATION	PROGENY			TOTAL	RATIO	P
		A-color*	White**	Yellow and Orange			
MAINE SUNSHINE, yellow	P_1			{ 15 p.y. { 63 yel.	78	3:1	.20
34520-6, red	P_1	157 red			157		
35009-5, red	P_1	{ 38 red { 12 salmon			50	3:1	.85
34520-6-12, red	P_1	35 red			35		
37117-37, light pink	P_1	23 l. pink			23		
33002-3, deep pink	P_1	{ 25 d. pink { 8 l. pink			33	3:1	.90
37531 = 34520-6 x M. S.	F_1	27 d. pink			27		
Three plants, deep pink	F_2	52	28	24	104	27:21:16	.25
38558 = 35009-5 x M. S.	F_1	{ 14 d. pink { 12 l. pink			26	1:1	.65
One plant, deep pink	F_2	57	20	19	96	9:3:4	.40
One plant, light pink	F_2	39	20	17	76	27:21:16	.25
38596 = 37117-37 x M. S.	F_1	13 l. pink			13		
Two plants	F_2	90	78	62	230	27:21:16	.60
38619 = 33002-3 x M. S.	F_1	{ 7 d. pink { 3 l. pink			10		
One plant, deep pink	F_2	71	23	26	120	9:3:4	.65
38637 = M. S. x 34520-6-12	F_1	23 d. pink			23		
One plant	F_2	164	59	73	296	9:3:4	.85
Two plants	F_2	152	115	75	342	27:21:16	.40

* The column for A-color includes salmon, red, light pink, and deep pink.
** The column for white includes white variegated red or pink.

aa. Yellow versus Anthocyanin.—

In Tables II and III are summarized the data from crosses between yellow and anthocyanin self-colored plants. The F_2 results conform to two different ratios, the 9:3:4 and the 27:21:16, indicating segregation for two and three genes respectively. It should be noted that in the crosses where segregation occurred according to the 27:21:16 ratio the yellow parents (MAINE SUNSHINE and 34006-2) were heterozygous for pale yellow, and that segregation according to the 9:3:4 ratio occurred in the same crosses. The pale yellow parent, 37039-14 in cross 38583, was a segregate from selfing 34006-2. Both plants selfed from this cross gave segregation according to the 27:21:16 ratio. On the other hand, the orange-yellow, 35003-1 (34518-1-1) and the yellow 34518-1-14 (Table VIII), were both from lines in which no pale yellow plants have ever been recorded. The seven F_1 plants that were selfed from these crosses all segregated according to the 9:3:4 ratio. Furthermore, the composition of the orange and yellow groups differed according to the nature of the segregation types. Whenever the segregation ratio was 9:3:4 the orange and yellow group was composed of

TABLE III

PARENTAGE	GENERATION	PROGENY			TOTAL	RATIO	P
		A-color*	White**	Yellow and Orange			
37039-14, pale yellow	P_1			15 p.y.	15		
34006-2, yellow	P_1			17 yel. 7 p.y.	24	3:1	.60
34518-1-14, yellow	P_1			24 yel.	24		
35003-1, orange-yellow	P_1			10 or. 3 yel.	13		
34520-6-12, red	P_1	35 red			35		
34520-6-13, red	P_1	40 red			40		
35019-1, light pink	P_1	13 l. pink 3 salmon			16	3:1	.60
33002-3, deep pink	P_1	25 d. pink 8 l. pink			33	3:1	.90
38559 = 35019-1 x 35003-1	F_1	7 d. pink 4 red			11		
Two plants, red	F_2	44 red 18 salmon	20	29	111	9:3:4	.90
Three plants, deep pink	F_2	127	49	48	224	9:3:4	.30
38564 = 34518-1-14 x 34520-6-12	F_1	12 red			12		
Two plants	F_2	152 red	37	67	256	9:3:4	.20
38605 = 34518-1-14 x 33002-3	F_1	14 d. pink			14		
Two plants	F_2	149	43	63	255	9:3:4	.70
38550 = 34006-2 x 33002-3	F_1	44 d. pink 9 l. pink			53	3:1	.18
One plant, deep pink	F_2	22	19	7	48	27:21:16	.20
One plant, deep pink	F_2	39	11	20	70	9:3:4	.65
One plant	F_2	51	28	25	104	27:21:16	.30
38583 = 34520-6-13 x 37039-14	F_1	22 d. pink			22		
Two plants	F_2	282	204	140	626	27:21:16	.40

* The column for A-color includes salmon, red, light pink and deep pink.
** The column for white includes white variegated red or pink.

only two types, namely, orange and yellow in the proportions of 3 orange to 1 yellow. Thus a more complete ratio for this type of segregation may be written: 9 A-colored: 3 white: 3 orange: 1 yellow. When, on the other hand, segregation occurred according to the 27:21:16 ratio the orange and yellow group consisted of three different types of individuals, namely, orange, yellow, and pale yellow in proportions approximating 9 orange : 3 yellow : 4 pale yellow.

These results suggest that the gene determining segregation either according to the 9:3:4 or the 27:21:16 ratios in this case is a member of the *Y*-*y* pair. That is, those F_1 plants that segregated according to the 9:3:4 ratio were homozygous for the *Y* gene, whereas those that segregated according to the 27:21:16 ratio were heterozygous for this gene. The third gene involved may be assumed to be a basic anthocyanin gene *A*, acting with the genes *Y* and *I* to produce normal anthocyanin color. The data on variegations (Section IV) indicate that no anthocyanin color

whatever is produced in the presence of its allele *a*, but that certain variegation patterns are possible with an intermediate allele a^{var}.

The interaction of these three gene pairs, all of which are necessary for full production of anthocyanin color, may be represented thus:

$\frac{Y}{y}\ \frac{I}{i}\ \frac{A}{a}$

27	*Y I A*	= A-colored	27	A-colored
9	*Y I a*	= white	21	white
9	*y I A*	= white		
3	*y I a*	= white		
9	*Y i A*	= transition group	16	yellow, orange, maroon
3	*Y i a*	= yellow		
3	*y i A*	= pale yellow		
1	*y i a*	= pale yellow		

In Table IV are summarized the data from the crosses between white and yellow in which the F_1 progenies were A-colored. On the basis of the genotypes suggested these data should conform to the 9:3:4 and 27:21:16 ratios. Although the progenies from these crosses are rather small, the segregations conform to these requirements.

TABLE IV

PARENTAGE	GENERATION	PROGENY			TOTAL	RATIO	P
		A-color*	White**	Yellow and Orange			
37079-21, white	P_1		20 white		20		
37079-29, white	P_1		30 white		30		
37109-1, white	P_1		23 white		23		
38192-14, yellow	P_1			27 yellow	27		
34520-17-35-12, salm. yellow	P_1			23 s. yel.	23		
MAINE SUNSHINE, yellow	P_1			63 yellow, 15 p. yel.	78		.20
39578 = 37109-1 x salm. yel.	F_1	7 l. p.			7		
One plant	F_2	32	29	29	90	27:21:16	.25
40552 = 37079-21 x salm. yel.	F_1	26 d. p.			26		
One plant	F_2	50	19	20	89	9:3:4	.75
40553 = 37079-21 x 38192-14	F_1	26 d. p.			26		
Two plants	F_2	65	39	33	137	27:21:16	.40
40526 = 38192-14 x 37079-29	F_1	28 d. p.			28		
Three plants	F_2	89	85	51	225	27:21:16	.30
40584 = M. S. x 37079-29	F_1	13 d. p.	7 white		20		
Two plants, white	F_2		52	14 p. yel.	66	3:1	.45
Two plants, deep pink	F_2	38	29	23	90	27:21:16	.85

* The column for A-color includes salmon, red, light pink, and deep pink.
** The column for white includes white and white-variegated.

b. White versus Anthocyanin.—

In Tables V and VI are summarized the results from crossing white with A-

TABLE V

PARENTAGE	GENERATION	PROGENY						TOTAL	RATIO	P
		A-color Group				White				
		Deep pink	Light pink	Red	Salmon					
IVORY, white	P_1					10		10		
37054-6, white	*									
37079-29, white	P_1					30		30		
34520-17-16, salmon	P_1				31			31		
34520-6-13, red	P_1			40				40		
37117-37, light pink	P_1		23					23		
38578 = 34520-6-13 x 37054-6	F_1	18						18		
Three plants	F_2	239		68		262		569	9:7**	.25
38579 = 34520-6-13 x IVORY	F_1	13		10				23	1:1	.50
One plant, deep pink	F_2	52		10		54		116	9:7	.50
One plant, red	F_2			92		63		155	9:7	.40
38617 = 37117-37 x 37054-6	F_1	13						13		
Two plants	F_2	102	24			92		218	9:7	.60
40531 = 34520-6-13 x 37079-29	F_1	20						20		
Two plants	F_2	96		24		48		168	3:1	.25
40569 = 34520-17-16 x 37079-29	F_1	26						26		
Three plants	F_2	70	26	22	11	52		181	3:1	.20

* 37054-6 was female sterile.

** All the A-color groups have been added together.

TABLE VI

PARENTAGE	GENERATION	PROGENY						TOTAL	RATIO	P
		Deep pink	Light pink	Red	Salmon	White var. A-col.	White			
34520-6-12, red	P_1			35				35		
34520-6-13, red	P_1			40				40		
34520-17-35-2, salmon	P_1				28			28		
37109-1, white	P_1						23	23		
38580 = 34520-6-13 x 37109-1	F_1	12		13				25	1:1	.80
Two plants, red	F_2			202		48	94	344	9:7	.35
Two plants, deep pink	F_2	93	42	20	5	49	97	306	9:7*	.20
38624 = 37109-1 x 37117-37	F_1	14	5					19		
Two plants, light pink	F_2		101			28	48	177	9:7	.80
Two plants, deep pink	F_2	68	21			30	43	162	9:7	.75
38624 = 37109-1 x 34520-6-12	F_1	13		12				25	1:1	.80
One plant, red	F_2			41	11	11	18	81	9:7	.15
One plant, deep pink	F_2	33		12		11	16	72	9:7	.25
One plant, deep pink	F_2	27	14	10	3	20	14	88	9:7	.35

* All the A-color have been added together against white and white-variegated.

colored. In the crosses 38578, 38579, 38580, 38624, 38625, and 38617, in which the white parents involved were pure white, never having shown any anthocyanin color whatever, all the F_2 populations grown conform to the 9:7 ratio, indicating segregation for two independent genes. The results from crosses 40531 and 40569, on the other hand, indicate a single gene difference. The white parent (37079-29) involved in these two crosses was occasionally slightly flushed with pink. It is the same plant that was discussed in connection with Table I.

In the process of purifying many of the original A-colored lines by selfing, numerous small progenies were obtained which segregated for white in the proportions of 3 A-colored to 1 white. Furthermore, many crosses were made between a number of whites selected from crosses 38578 and 38579 (Table V). These F_1 progenies contained all possible combinations, namely, all white, 3 white to 1 A-colored, 1 white to 1 A-colored, or all A-colored.

In most of the crosses between pure white and full A-color, between yellow and full A-color, and between yellow and white that resulted in full anthocyanin color, some of the whites occasionally were tinted pink or red and in some, whose products indicated segregation for both *y* and *a*, a goodly number of the progeny were strongly flushed pink or red on white background. One plant (37079-29) that occasionally produced a faint tinge of color in the petals has already been discussed in connection with Tables I and V. This plant, when crossed to two different yellow plants, produced colored F_1 progenies (Table IV) which in the next generation (F_2) segregated for white and yellow in 27:21:16 proportions; that is, segregation by three genes. On the other hand, when it was crossed to pale yellow (Table I), the result was a white F_1 and segregation only for pale yellow in the second generation in proportions indicating segregation by only one gene. Likewise, when crossed to homozygous salmon and red, the F_2 results indicated segregation by one gene (Table V). The only genotype possible that would account for these results is *y I A*.

As already stated, many crosses were made among whites selected from the F_2 generations from crosses 38578 and 38579 (Table V). Several of these plants, including some that were lightly tinted, were crossed to 37079-29 and some of its self-seedlings. In every case tinged selections, when mated to 37079-29 or its self-seedlings, produced only tinged progeny. On the other hand, the same selections produced colored progeny when mated to certain pure whites with which 37079-29 also produced colored progenies, suggesting that the tinge or flush of color was inherent in the *y*-gene or some allele to it. As different whites of known genotypes gradually became available, numerous crosses were made in order to test this hypothesis. The results (Table XVI, p. 60) bear out the hypothesis that the tinged and flushed plants belong to the *y*-whites.

As may be seen in figs. 2–4 of plate 9, the anthocyanin in the flushed individuals varies not only in amount but also in distribution. In matings between strongly flushed plants and near-whites the colors of the F_1 generations usually were intermediate, but sometimes they were stronger than in either parent. How-

ever, as it has not yet been possible to grow such progenies under controlled conditions in the greenhouse, it is not known whether this increased color was due to the genotype or the environment.

In the early stages of this study, when many lines were inbred in order to provide homozygous plants, numerous lines were obtained whose segregations indicated that white flushed with anthocyanin is a simple recessive to full self-color and a simple dominant to that type of whites which produce a slight tint or flush of color only under favorable conditions. The monogenic relationship between white-flushed anthocyanin and the corresponding self-color is further demonstrated by the crosses between flushed and variegated individuals (Tables XVII and XIX).

On the basis of the results obtained so far, it can be said that the lowest allele of *y* that has been obtained to date, may with *I* and *A* produce a faint tinge or flush of anthocyanin on the petals of the flower. The anthers and the tips of the stigmas are usually faintly colored in this type, even when the petals are white. The intensity of color varies with the specific genotype and the environmental conditions. Usually *y*-whites with *R* can be distinguished from *r* plants but whether a plant has the dominant allele of *S* or *M* cannot be determined except by breeding tests. The gene for flushing has been designated y^{fl}. Probably different alleles of it exist, and perhaps also one or more modifying genes that influence its expression.

The occurrence of white variously striped with A-color in many of the crosses is discussed in Section IV.

II. THE CYANIC GROUP

a. Pelargonidin Monoglycoside Colors.—

In 1933 a red seedling, which, because of sparse pollen production, could not profitably be selfed, was pollinated by SPECTRUM SUPREME, a commercial red variety which only rarely sets seeds (due to the prevalence of secondary ovaries) but usually produces good pollen. All F_1 plants were red (Table VII). Three of the four F_1 plants that were selfed segregated in the proportions of 9 red : 3 salmon : 3 salmon-orange : 1 salmon-yellow, while the fourth did not segregate. In the F_3 one red plant again segregated in this manner, another red segregated for salmon in the proportions of 3 red : 1 salmon, while the third red did not segregate. Of the three salmon plants selfed in this generation two segregated for salmon-yellow in the proportions of 3:1, while the third bred true, as did also the only salmon-yellow plant selfed. In the F_4 the salmons either segregated for salmon-yellow or bred true. The two salmon-yellows that were selfed bred true.

These results, together with those from the crosses 38610, 39525 and 39583 summarized at the bottom of Table VII, clearly demonstrate the difference in one gene between red and salmon, red and salmon-orange, salmon and salmon-yellow, salmon-orange and salmon-yellow, but a difference of two genes between red and yellow. The presence of orange and yellow indicated segregation for the *i* gene

TABLE VII

PARENTAGE	GENERATION	PROGENY				TOTAL	RATIO	P
		Red	Salmon	Salmon-orange	Salmon-yellow			
33511-3, red	No P_1	3				3		
SPECTRUM SUPREME, red	No P_1							
38187-10, salmon	P_1		37			37		
34520 = 33511-3 x SPECTRUM SUPREME	F_1	23				23		
34520-3, red	F_2	10	8	4	2	24	9:3:3:1	.25
34520-6, red	F_2	157				157		
34520-10, red	F_2	83	24	31	8	146	9:3:3:1	.80
34520-17, red	F_2	125	43	28	12	208	9:3:3:1	.25
34520-17-2, salmon	F_3		32		12	44	3:1	.70
34520-17-5, red	F_3	40	13			53	3:1	.90
34520-17-6, red	F_3	43	19	12	4	78	9:3:3:1	.60
34520-17-8, red	F_3	79				79		
34520-17-16, salmon	F_3		31			31		
34520-17-19, salm. yel.	F_3				12	12		
34520-17-35, salmon	F_3		26		10	36	3:1	.70
34520-17-35-1, salmon	F_4		25		9	34	3:1	.80
34520-17-35-2, salmon	F_4		28			28		
34520-17-35-12, salm. yel.	F_4				23	23		
34520-17-35-31, salm. yel.	F_4				27	27		
38610 = 34520-6 x 34520-17-35	F_1	24				24		
Two plants	F_2	193	61			254	3:1	.70
F_1 x 34520-17-35-2	BC	64	55			119	1:1	.45
F_1 x 34520-17-35-12	BC	27	31			58	1:1	.60
39525 = -17-35-1 x 17-35-12	BC		29		26	55	1:1	.65
39583 = 34520-6 x 38189-10	F_1	12				12		
Three plants	F_2	162	62			224	3:1	.50

(see under III). Chemical determinations have shown the anthocyanin in both red and salmon to be a monoglycoside of pelargonidin, but in different concentrations (Geissman and Mehlquist, '47). The genes corresponding to these different concentrations have been designated *S* and *s* respectively. Red, or scarlet as this color often is called in commercial carnation culture, may thus be designated by the genotype *Y I A S* while salmon would be *Y I A s*.

Results from a similar cross are summarized in Table VIII. The F_2 segregations here are in the same proportions as those just discussed, but one of the genes involved is different. The presence of yellow and orange-yellow again indicates segregation for the *i* gene. The presence of white but absence of pale yellow indicates segregation for a gene of the *A* locus. All the whites from this cross had from one to many narrow red stripes. The yellows were at first recorded as pure yellow but a closer examination revealed occasional faint reddish stripes. No such stripes were ever found in the orange-flowered group. When a yellow from this cross was mated to a red from a line in which no reddish stripes had ever been observed (cross 38564, Table IX) all the whites in the F_2 had occasional red

TABLE VIII

PARENTAGE	GENERATION	PROGENY				TOTAL	RATIO	P
		Red	White var. red	Orange	Yellow var. red			
33506-3, red	No P_1							
33514-11, red	No P_1							
34520-6, red	P_1	157				157		
34518 = 33506-3 x 33514-11	F_1	14				14		
Two plants, red	F_2	137	57	38	12	244	9:3:3:1	.20
Three plants, red	F_2	170	66			236	3:1	.30
34518-1-1, orange	F_3			10	3	13	3:1	
34518-1-12, white var. red	F_3		26		8	34	3:1	.80
34518-1-13, white var. red	F_3		18		8	26	3:1	.50
34518-1-14, yellow var.	F_3				24	24		
34518-9-2, white var. red	F_3		38			38		
34518-9-2 x 34518-1-1	F_4	18	17			35	1:1	
34518-1-14 x 34518-9-2	F_4		2*			2		
#1 from above cross	F_5		65		20	85	3:1	.75
#2 from above cross	F_5	1	69		23	93	3:1	.95
#2 red mutant	F_5		51		23	74	3:1	.20
34518-1-12 x 34518-1-13	F_4		7*		2	9	3:1	
One plant from above	F_5		42		22	64	3:1	.07
Red mutant	F_5		48		18	66	3:1	.60
38546 = 34518-1 x 34520-6	F_1	55				55		
38546-5, red	F_2	49	15	13	6	83	9:3:3:1	.85
38546-6, red	F_2	65	15			80	3:1	.20

* One plant of each of these lots produced red-flowered branches which were vegetatively propagated and then self-pollinated.

stripes; most of the yellows had faint reddish stripes; but none of the orange was ever recorded as having them. For reasons discussed under section IV this gene for white with red stripes must be considered an allele in the *A-a* series.

As in cross 34520 (Table VII) red differs from yellow in two genes whereas there is a single gene difference between red and white, red and orange-yellow, orange-yellow and yellow, and white and yellow.

The red of cross 34518 was somewhat duller or more toward the salmon-red hue than the red from cross 34520. When crosses were made between reds from these different families the F_1 plants were always dull red and in the F_2 generations the deeper red of the 34520 line reappeared. However, adverse weather conditions made accurate classification difficult. Somewhat less than one-fourth of the progeny was classified as deep red, and of the remainder some were distinctly dull red and many appeared to be intermediate. Lately a still deeper red has appeared in one line derived from the cross 38579 (Table V). Again, this red totaled about one-fourth, whereas the remainder was apparently all the kind just discussed as deep red. For the purpose of reference, the red from cross 34520 has been designated "standard" red, while the dull red, deep red, and any other red that might be met with in future work will be measured against this standard.

When the salmon-orange from 34520 was crossed to the orange from 34518 the F_1 was orange and the salmon-orange reappeared in the F_2 to the extent of about one-fourth of the total. When yellow from 34518 was crossed to salmon-yellow from 34520, the F_1 was orange and the F_2 was approximately 9 orange to 7 yellow. The orange here contained orange, salmon-orange and what appeared to be intermediate shades. Likewise, the yellow group contained both clear yellow and salmon-yellow.

The single gene difference between dull red and standard red, between standard red and deep red, as well as between orange and salmon-orange might be due either to different alleles of the S gene or to an independent modifying gene determining the intensity of the anthocyanin. However, when crosses were made between various derivatives of crosses 34518 and 34520 (Table IX) all the F_1 were dull red and the F_2 included not only dull red and deep red but also salmon. From these observations it must be concluded that the varying shades of red are not due to multiple alleles of the S gene but rather to an independent modifying gene influencing the concentration of the anthocyanin. Further work is necessary

TABLE IX

PARENTAGE	GENERATION	PROGENY					TOTAL	RATIO	P
		Red	Salmon	White var. red	Orange	Yellow			
34520-6-12, red	P_1	35					35		
34520-17-16, salmon	P_1		30				30		
34520-17-19, salm. yel.	P_1					12	12		
34520-17-35, salmon	P_1		26			10	36		
34520-17-35-12, salm. yel.	P_1					23	23		
34518-1-12, white var. red	P_1		26			8	34		
34518-1-14, yellow var. red	P_1					24*	24		
34518-1-17, orange	No P_1								
38565-2, white var. red	P_1			70		23*	92	3:1	.95
38566 = 34518-1-14 x 34520-17-35	F_1	13			3		16	3:1	.60
Two plants, red	F_2	83	23	27	35**		168	27:9:12:16	.60
Two plants, orange	F_2				30	22	52	9:7	.80
38574 = 34520-17-16 x 34518-1-12	F_1	24					24		
Two plants, red	F_2	86	29	29			144	9:3:4	.30
Six plants, red	F_2	142	50	60	85**		337	27:9:12:16	.95
38574 = 34520-17-16 x 34518-1-17	F_1	15					15		
Two plants, red	F_2	110	32		42**		184	9:3:4	.60
One plant, red	F_2	40	9	12	14		75	27:9:12:16	.30
38564 = 34518-1-14 x 34520-6-12	F_1	12					12		
Two plants, red	F_2	152		37	67**		256	9:3:4	.20
39504 = 39520-17-19 x 38565-2	F_1	32			30		62	1:1	.80
39554 = 34520-17-35 x 38565-2	F_1	39			33		72	1:1	.95

* These yellows were lightly variegated red.
** The field conditions did not permit accurate separation of yellow from orange.

before the gene or genes causing these differences can be properly identified.

The results, summarized in Table IX, in all other respects confirm the conclusions based on the data from Tables VII and VIII.

aa. Pelargonidin Diglycoside Colors.—

In Table X are summarized the results of the crosses made between red and deep pink, red and light pink, light pink and deep pink, and salmon and deep pink. One of the crosses between red and salmon from Table VII is included for comparison. It is evident that deep pink and light pink differ from red and salmon respectively in one gene and that deep pink differs from salmon in two genes, the salmon being the double recessive while deep pink is the double dominant.

Chemical determinations have shown that the deep pink and light pink are due to a pelargonidin which is not a monoglycoside, as was red and salmon, but a diglycoside. Thus the gene that differentiates deep pink from red and light pink

TABLE X

PARENTAGE	GENERATION	PROGENY				TOTAL	RATIO	P
		Deep pink	Light pink	Red	Salmon			
33002-3, deep pink	P_1	70				70		
37117-37, light pink	P_1		27			27		
34520-6-12, red	P_1			35		35		
34520-6-13, red	P_1			40		40		
34520-17-16, salmon	P_1				30	30		
37010-1-12, salmon	P_1				24	24		
38610 = 34520-6-13 x 34520-17-16	F_1			24		24		
Two plants	F_2			193	61	254	3:1	.70
F_1 x salmon parent	BC			91	88	179	1:1	.70
39583 = 34520-6-13 x 37010-1-12	F_1			13		13		
Three plants	F_2			173	63	236	3:1	.50
F_1 x salmon parent	BC			81	77	158	1:1	.75
38609 = 34520-6-13 x 34002-3	F_1	47				47		
Six plants	F_2	99		39		138	3:1	.35
F_1 x red parent	BC	87		90		177	1:1	.80
38621 = 37117-37 x 34002-3	F_1	37				37		
Three plants	F_2	84	29			113	3:1	.85
F_1 x light pink parent	BC	63	59			122	1:1	.70
38620 = 33002-3 x 34520-17-16	F_1	14				14		
Two plants	F_2	88	31	26	12	157	9:3:3:1	.90
F_1 x salmon parent	BC	129	115	110	92	446	1:1:1:1	.30
38597 = 37117-37 x 34520-6-12	F_1	19				19		
Four plants	F_2	70	19	20	7	116	9:3:3:1	.80
F_1 x salmon (34520-17-16)	BC	39	44	38	43	164	1:1:1:1	.85
38622 = 34520-6-12 x 37117-37	F_1	25				25		
Two plants	F_2	100	35	38	11	184	9:3:3:1	.90
F_1 x salmon (34520-17-16)	BC	77	57	78	56	268	1:1:1:1	.08

from salmon apparently does so by causing the development of a diglycoside instead of a monoglycoside. This gene has been designated *M*. Then the genotype of deep pink is *Y I A S M*, light pink *Y I A s M*, red *Y I A S m* and salmon *Y I A s m*. The diglycosidic anthocyanin apparently is less stable than the corresponding monoglycoside, for in strong sunlight deep pink and light pink bleach much more than red and salmon. In fact, under California field conditions, the light pinks often bleach to almost white whereas the salmons retain their color fairly well.

The same differences in intensity of color noted for the reds and salmons obtain in the deep pinks and light pinks. In all probability, the same genes are responsible for the differences in both series of colors.

b. Cyanidin Monoglycoside Colors.—

Table XI gives the results of crossing red with crimson. Unfortunately, neither of the crimson plants used as parents was homozygous for crimson but the fact that the F_2 progenies contain variegated individuals as well as crimson and red does not obscure the monogenic relationship between these two colors. Only one cross between salmon and crimson is available so far. The crimson was heterozygous for maroon-variegated-crimson and the salmon was heterozygous for salmon-yellow. As shown in Table XII, the F_1 consisted of 21 crimson and 4

TABLE XI

PARENTAGE	GENERATION	PROGENY				TOTAL	RATIO	P
		Crimson	Red	Maroon var. crimson	Orange var. red			
34520-6-13, red	P_1		40			40		
37107-2, crimson	P_1*							
37107-3, crimson	P_1	17		8		25	3:1	.45
37107-3-9, maroon var. crimson	P_1			19	6	25	3:1	.80
37107-3-20, crimson	P_1	39		11		50	3:1	.60
37107-3-24, crimson	P_1	29		11		40	3:1	.70
38581 = 34520-6-13 x 37107-2	F_1	13	11			24	1:1	
38581-13, crimson	F_2	62	22	29	7	120	9:3:3:1	.45
38581-21, crimson	F_2	105	35			140	9:3:3:1	1.00
38581-22, red	F_2		75			75		
38581-23, crimson	F_2	115	38	50	12	215	9:3:3:1	.50
38581-13 x red parent	BC	26	29			55	1:1	.65
38581-21 x red parent	BC	26	22			48	1:1	.50
38582 = 34520-6-13 x 37107-3	F_1	14				14		
38582-2, crimson	F_2	72	19			91	3:1	.35
38582-8, crimson	F_2	152	39	45	10	246	9:3:3:1	.12
39516 = 34520-6-13 x 37107-3-9	F_1	16				16		
Two plants, crimson	F_2	64	20	20	6	110	9:3:3:1	.90
39516-1 x variegated parent	BC	39	11	37	9	96	3:1:3:1	.75

* Complete P_1 segregation for 37107-2 was 35 crimson, 8 red, 8 maroon var. crimson, 2 orange var. red, 10 lavender, 2 salmon.

TABLE XII

PARENTAGE	GENERATION	PROGENY									TOTAL	RATIO	P
		Crimson	Maroon var. crimson	Maroon	Lavender	Salmon	Red	Orange var. red	Orange	Salmon-yellow			
34520-17-35, salmon	P_1					26				10	36	3:1	.70
34520-17-35-1, salmon	P_1					25				9	34	3:1	.80
34520-17-35-2, salmon	P_1					28					28		
37107-3, crimson	P_1	17	8								27	3:1	.45
37107-3-9, maroon var. crimson	P_1		19					6			25	3:1	.80
38587 = 37107-3 x 34520-17-35	F_1	21	4								25	3:1	.08
38587-5, crimson	F_2	137		37	27	8	41		11	3	264	27:9:9:3:16*	.01
38587-10, crimson	F_2	85	24		23	9	25	10			180	27:9:9:3:16	.40
38587-24, maroon var. crimson	F_2		56	7				13	7	3	86	3:1**	.20
38587-24 x 34520-17-35-2	BC	17			11	14	11				53	1:1:1:1	.60
39518 = 37107-3-9 x 34520-17-35-1	F_1	2	2								4		
Two plants, crimson	F_2	96	26		25	7	31	9			194	27:9:9:3:16	.15
One plant, maroon var. crimson	F_2		58	17				22	7		104	9:3:3:1	.85

* This ratio is based on the adding of all the members of the transition group. The crimsons in this population were very vigorous while the members of the transition group were very poor.

** The ratio is based on variegated versus non-variegated plants. The population is too small to warrant any further treatment.

maroon-variegated-crimson. Only two crimsons and one maroon-variegated-crimson were selfed. As both the maroons and the variegated types are members of the transition group, only crimson, red and lavender need to be considered here. Although the proportions of lavender and salmon are somewhat too small, the reasonably good fit to a 9:3:3:1 ratio suggests that two pairs of independent genes are involved. The back-cross 39552, although small, supports this hypothesis. Since the genotypes for red and salmon are respectively *Y I A S* and *Y I A s*, the genotype for crimson and lavender may be written *Y I A S R* and *Y I A s R*, the gene for crimson being designated by *R*. When three lavender plants from this cross were selfed, they segregated for salmon in the proportions of 3 lavender to 1 salmon, and when lavender was crossed to red the F_1 result was crimson. This is just what would be expected on the basis of the genotype suggested.

The anthocyanin in both the crimsons and the lavenders has proved to be a monoglycoside of cyanidin. The function of the *R* gene then apparently is the production of cyanidin to the exclusion of pelargonidin, whereas in the presence of *r* pelargonidin only is produced.

bb. Cyanidin Diglycoside Colors.—

When a crimson that was heterozygous for maroon-variegated-crimson was crossed to a homozygous deep pink the F_1 generation was magenta-purple (Table XIII). The anthocyanin present in this magenta-purple proved to be a diglycoside of cyanidin. Thus, the gene *M* introduced through the deep pink parent functions also here as a modifying gene concerned with the development of the corresponding diglycoside. The independence of *M* with respect to *R* and *S* is clearly shown in Table XIII. The only genotype left in this series which has not been accounted for is *Y I A s R M*. This was produced by crossing light pink *Y I A s r M* with lavender-pink *Y I A s R m*. The F_1 appeared to be slightly paler than the lavender-pink parent but in the F_2 generation it was impossible, by inspection, to separate accurately the plants having *M* from those having the recessive allele *m*, but chemically they proved quite distinct. All plants with the gene *M* contained

TABLE XIII

PARENTAGE	GENERATION	PROGENY						TOTAL	RATIO	P
		Purple	Crimson	Deep pink	Red	Maroon var. crimson	Orange var. red			
33002-3, deep pink				70				70		
34520-6-12, red	P_1				35			35		
37107-3, crimson	P_1		17			8		25	3:1	.45
38603 = 37107-3 x 33002-3	F_1	9						9		
38603-2, purple	F_2	23	9	6	2	11	3	54	27:9:9:3:12:4	.90
38603-8, purple	F_2	143	46	35	12			236	9:3:3:1	.30
38603-9, purple	F_2	26	6	13	3			48	9:3:3:1	.25
Total for -8 and -9	F_2	169	52	48	15			284	9:3:3:1	.65
38603-8 x 34520-6-12	BC	70	79	66	85			300	1:1:1:1	.25

a diglycoside while those with its recessive allele *m* contained the corresponding monoglycoside.

III. The Transition Group

The results summarized in Table VII show that salmon-yellow differs from red in two genes, but only in one gene from either salmon or orange. One of these genes must be *i*, as otherwise yellow could not be expressed since *I* has been shown to be epistatic to *Y*. The other gene must be *s*, since this yellow could be obtained as a segregate by selfing salmon heterozygous for *i*. The genotype of this yellow then must be *Y i A s*, and since salmon has already been shown to be *Y I A s*, the only genotype possible for salmon-orange is *Y i A S*. On the basis of these genotypes all segregations shown in Table VII are possible.

The yellow in Table VIII likewise differs from red in two genes. For the reasons stated in the preceding paragraph one of these genes must be *i*. The other could be an allele of *A* since segregation also took place for white, or near-white, but no pale yellow; it might also be a new gene. However, when white-variegated red plants from this source were crossed to plants known to be *Y I a* or *y I a* the F_1 were always white-variegated red or white-variegated deep pink, but when they were crossed to *y I A* plants the F_1 progenies were fully anthocyanin-colored and segregated in the F_2 in the proportions of 9 A-colored : 3 white-variegated : 4 white. This second gene then must be a member of the *A-a* series. The genotype for this yellow might tentatively be represented thus: *Y i* a^{var} *S*.

When this yellow was crossed to the salmon-yellow from 34520 the resulting F_1 was intermediate between the salmon-orange of 34520 and the orange-yellow of 34518 but more like the latter. The F_2 consisted of apparently 9 orange to 7 yellow. The orange group contained orange-yellow, salmon-orange, and what appeared to be intermediate shades. The yellow group likewise contained both yellow and salmon-yellow. Most of the clear yellows had faint reddish stripes but none were found on any of the salmon-yellows or on any member of the orange groups.

Chemical determinations made on different salmon-oranges and orange-yellows showed that the color in both groups was due largely to a non-anthocyanin substance plus a small amount of anthocyanin probably of the pelargonidin groups. However, it has not yet been possible to determine whether or not the difference between these groups is due to a difference in concentration of one or both pigments.

When salmon-yellow and orange were obtained as segregates from crimson and purple (Table XII), segregation for two other members of the transition group, maroon and pale maroon, also occurred in proportions suggesting a ratio of 9 maroon : 3 pale maroon : 3 orange : 1 yellow. On subsequent selfing some of the maroons repeated this segregation, but pale maroon and orange, on selfing, either bred true or segregated for salmon-yellow only. The genotype of the maroon must therefore be *Y i A S R*, and the pale maroon *Y i A s R*. Chemical determinations have shown these colors to be due to a combination of anthocyanin, probably of the cyanidin type, and a non-anthocyanic substance.

Whether or not a member of the transition group has the *M* or *m* allele cannot be determined except by genetical tests. The amount of anthocyanin is evidently so small that the difference between a mono- and a diglycoside cannot be determined by inspection.

IV. The Variegated Group

a. Random Narrow Variegation

The first type of variegation to appear in these studies was that shown in pl. 9, figs. 5 and 6. We have termed it *random narrow* because of the narrow, well-defined stripes which are more or less randomly distributed, although they sometimes tend to be concentrated toward the distal ends of the petals. Variegated lines show considerable variation in the amount of striping, from an average of less than 1 stripe per petal up to as many as 20 or more. Occasionally a whole petal or even a whole flower is colored. The color of the stripes is determined by the genotype of the self-colored normal type from which segregation takes place; that is, if this type of variegation segregates from a red-flowered line the stripes are red, from a deep pink line the stripes are deep pink, and so on. Variegation of this type has been obtained from all of the anthocyanin colors. The background color is ordinarily white though it may be yellow. If yellow, the stripes are usually so faint that they often escape attention unless the flowers are carefully examined.

Whenever this type of variegation has segregated from normal self-color the proportions have always been such as to indicate a monogenic difference between variegation and self-color. All individuals variegated on white ground that have been selfed have either bred true or segregated for pure white, or yellow faintly striped with the same anthocyanin color or one recessive to it (see Table VIII). The results from crossing plants with this type of variegation with plants of known genotypes are shown in Table XIV.

Although the F_2 data from the crosses listed in Table XIV are as yet very meagre, they do support the hypothesis alluded to in sections Ib and IIa, namely, that this type of variegation is due to a gene which is allelic to the *A*-*a* pair. That is: A = full color, a = pure white; while a^{var} permits the development of fully colored narrow stripes of anthocyanin on white background, or, in conjunction with *i*, faintly colored stripes on yellow background. The monogenic relationship between full self-color and white-variegated is definitely demonstrated by the crosses summarized in Table VIII.

Apparently different alleles of a^{var} exist, or the expression of this gene is modified by other genes, for through selection it has been possible to select lines of white-variegated that differ only in the amount of variegation. When such lines have been intercrossed the F_1 generations have generally been intermediate, but in the F_2 generations the variegation range sometimes exceeded that of both parents. That is, in the F_2 from a cross between heavily variegated and lightly variegated the range was extended from very lightly to very heavily variegated. This increase might be due only to natural variation in the expression of the gene for variega-

TABLE XIV

CROSS			RESULTS
Unknown	Known		
	Color	Genotype	
White variegated red x	White	*yIASrm*	Red
" " " x	"	*yIASRm*	Crimson
" " " x	"	*yIASrM*	Deep pink
" " " x	"	*yIaSrm*	White var. red
" " " x	"	*YIaSRm*	" " crimson
" " " x	"	*YIaSrM*	" " deep pink
" " " x	"	*yIaSrm*	" " red
" " " x	"	*yIaSrM*	" " deep pink
" " " x	Orange	*YiASrm*	Red
" " " x	"	*YiASrM*	Deep pink
" " " x	Salmon-yellow	*YiAsrm*	Red
" " " x	Yellow	*YiaSrm*	White var. red
" " " x	"	*YiaSrM*	" " deep pink
" " " x	Pale yellow	*yiaSrM*	" " deep pink
Yellow* " " x	White	*yIASrm*	Red
" " " x	"	*YIaSrm*	White var. red
" " " x	Orange	*YiASrm*	Orange
" " " x	Yellow	*YiaSrm*	Yellow var. red
" " " x	Pale yellow	*yiaSrM*	" " pink

* These yellow-variegated-red were only faintly variegated but the F_1 with *YIaSrm* was quite well striped with red. All the yellow-variegated-red plants that were used in these crosses were segregates from red.

TABLE XV

CROSS			RESULTS
Unknown	Known		
	Color	Genotype	
Orange variegated red	x Red	*YIASrm*	Red
" " "	x Orange	*YiASrm*	Orange var. red
" " "	x Maroon	*YiASRm*	Maroon var. crimson
" " "	x Yellow	*YiaSrM*	Orange var. deep pink
" " "	x Pale yellow	*yiaSrM*	Orange var. deep pink
Maroon " crimson	x Red	*YIASrm*	Crimson
" " "	x Orange	*YiASrm*	Maroon var. crimson
" " "	x White var. crim.	$YIa^{var}SRm$	Crimson
Yellow " white	x Yellow	*YiaSrM*	Yellow var. white
" " "	x Orange	*YiASrm*	Orange var. deep pink
" " "	x Maroon	*YiASRm*	Maroon var. purple
" " "	x Crimson	*YIASRm*	Purple
Orange " red	x White	*yIASrm*	Red
" " "	x "	*yIASRm*	Crimson
" " "	x "	*YIaSrm*	Red
" " "	x "	*YIaSrM*	Deep pink
" " "	x "	*yIaSrM*	Deep pink
" " "	x White var. red	$YIa^{var}Srm$	Red
Yellow " white	x "	*yIASrm*	Deep Pink
" " "	x "	*YIaSrm*	White
" " "	x "	*yIaSrM*	White
" " "	x Yellow var. red	$Yia^{var}Srm$	Yellow var. white and red

tion, or it might be the result of other genes modifying the expression of the variegation gene.

F_1 generations between homozygous white-variegated and pure white (*a*-white) have always been white-variegated. The limited F_2 generations that have been grown so far from such crosses have indicated segregation for one or two genes although usually there tends to be an excess of whites. This excess is probably due to the bleaching of the anthocyanin stripes under field conditions. At any rate, plants that have been classified in the field as pure white sometimes proved to be variegated when transferred to the greenhouse during the fall and winter. Two such plants selfed in the greenhouse segregated for pure white, so it must be assumed that they actually were of the $\frac{a^{var}}{a}$ genotype.

The crosses summarized in Table I are of interest in this connection. The plant 37054-6 was a pure white that had remained so under all conditions in or out of the greenhouse. When it was crossed to a yellow faintly variegated pink the F_1 (30 plants) was white with deep pink stripes. In the F_2 generation it was impossible to separate definitely the variegated and non-variegated in the yellow group but in the white group considerable care was taken to check the plants from time to time in order to ascertain the exact proportion of variegated individuals. The final count of 95 variegated to 85 non-variegated indicates segregation for two genes giving a 9:7 ratio.

The plant 37054-6, on the basis of its behavior in other crosses (see Table V), must be assumed to be of the $\frac{y}{y}\frac{I}{I}\frac{a}{a}\frac{S}{S}\frac{r}{r}\frac{M}{M}$ genotype. The other plant (37075-14) was $\frac{Y}{Y}\frac{i}{i}\frac{a^{var}}{a^{var}}\frac{S}{S}\frac{r}{r}\frac{m}{m}$. Therefore, with respect to variegation we should expect from this cross the following genotypes: $9\ Y\ a^{var} : 3\ Y\ a : 3\ y\ a^{var} : 1\ y\ a$, of which only the first should be variegated.

Another pure white plant 37109-1 was crossed to a pure yellow, probably of the genotype $\frac{Y}{Y}\frac{i}{i}\frac{a}{a}$. The result (40522, Table I) was 13 white-variegated and 14 white. As in the previous cross it was impossible to classify the yellows in the F_2 generation into variegated and non-variegated plants, but in the white group from selfing two variegated plants, 48 were classified as variegated and 30 as non-variegated, again indicating segregation for two genes. The one non-variegated plant that was selfed produced non-variegated plants only. From other crosses it had been established that the most likely genotype for 37109-1 was $\frac{y}{y}\frac{I}{I}\frac{a^{var}}{a}\frac{S}{s}\frac{r}{r}\frac{M}{m}$. The results obtained from this cross are in agreement with these genotypes. When this white was crossed to another yellow which, as far as can be ascertained, was also of the genotype *Y i a*, the F_1 contained 27 lightly variegated to 18 non-variegated. In the F_2 there was a considerable deficiency in the variegated group which in all probability was due to bleaching so that some lightly variegated plants were classified as white. When the same white was

crossed to homozygous red (crosses 38580 and 28625, Table VI) lightly variegated individuals again occurred in the F_2, but, as may be seen from the table, the variegated proportion is less than expected. The same occurred when MAINE SUNSHINE, a commercial yellow variety, was crossed to red (cross 38637, Table II) or to a white of the *y*-type resulting in a deep pink F_1 (cross 50584, Table IV). In either case lightly variegated individuals occurred in the F_2 generation but in somewhat smaller proportions than would be expected on the basis of the genotype suggested.

b. Random Broad Variegation.—

This type of variegation (pl. 10, fig. 4) was first met with in crosses involving the commercial yellow carnation MAINE SUNSHINE. This variety, although generally classified as a self-colored yellow, occasionally produces faint pink stripes such as described under IVa. It was therefore no surprise to find individuals in the F_2 with narrow stripes of full anthocyanin color on yellow or white ground. However, in addition many individuals were obtained with randomly distributed stripes that were much broader and less definitely delimited than in the *random narrow* variegation described above. The color in this type of variegation ranges from yellow striped with white up to maroon striped with purple. Thus this type of variegation is limited to the transition series. Now, since all the members of this series are *i i*, it seemed logical to assume that the gene responsible for this type of variegation may have been a multiple allele of the *I-i* series.

The results of crosses between members of this variegation series and plants of known genotypes are shown in Table XV. Although the number of F_2 populations raised to date from the crosses listed in Table XV are few, the results indicate that each member differs in one gene only from the corresponding self-colors. That is, maroon-var.-crimson behaves in a simple recessive with respect to crimson but as a simple dominant to maroon; orange-var.-red bears a similar relation-

TABLE XVI

CROSS			RESULTS
Unknown	Known		
	Color	Genotype	
White flushed pink*	x White	*YIaSrm*	Red or deep pink
" " "	x "	*YIaSrM*	Deep pink
" " "	x "	*YIaSRm*	Crimson or purple
" " "	x "	*yIASrm*	White flushed pink
" " "	x "	*yIASrM*	" " "
" " "	x "	*yIASRm*	" " purple
" " "	x "	*yIaSrm*	" " pink
" " "	x "	*yIaSrM*	" " "
" " "	x Yellow	*Yia*---	Red or deep pink
" " "	x Pale yellow	*yia*---	White flushed pink

* It is difficult to distinguish between *m* and *M* types in this group. Except in heavily flushed individuals red and pink flush gives the same appearance. Some of the flushed plants used here had *M*, others *m*.

ship to red and orange. The only yellow-variegated-white that has been obtained so far showed a corresponding relationship to yellow and *a*-white. The cross to *y*-white gave full self color. The results obtained (Tables XI, XII, XIII and XV) are all compatible with the hypothesis that this type of variegation is due to a gene multiple allelomorphic to the *I-i* series. That is, I = full color; i^{var} = broad random variegation; i = self-color of the transition series.

The most interesting cross in this group is one between yellow broadly variegated white and yellow faintly variegated narrow red. Seven of the 17 F_1 plants were yellow faintly variegated red, but the other 10 had both broad white stripes and narrow pink stripes. Furthermore, where the two types of variegation overlapped (that is, where the narrow stripes overlapped the broad) the narrow stripes were of a bright deep pink color; but when the narrow stripes were between the white stripes (that is, on yellow ground) they were as faint as in the parent from which they were introduced. Thus it is evident that wherever the white stripes do occur the conditions are the same as if the whole flower had been *I* instead of i^{var}.

c. Picotee Pattern.—

This variegation pattern (pl. 10, figs. 1–3) appeared in an F_2 population from a cross between a commercial crimson (WOBURN) and a commercial white (MATCHLESS) of the *y*-series. The F_1 contained only 12 plants of which 3 were

TABLE XVII

PARENTAGE	GENERATION	PROGENY				TOTAL	RATIO	P
		Self-color	White var. red	White flushed red	White			
37030-6, white flushed red	P_1			33		33		
37079-18, white*	P_1				26	26		
37030-16, white var. red rand. nar.	P_1		27			27		
37078-11, " " " " "	P_1		29			29		
38201-4, " " " " "	P_1		23			23		
40529 = 38201-4 x 37030-6	F_1	23				23		
Three plants, red	F_2	150	58	70		278	9:3:4	.60
40532 = 37030-6 x 37078-11	F_1	8				8		
Two plants, red	F_2	53	21	38		112	9:3:4	.05
40536 = 37030-16 x 37030-6	F_1	19				19		
Three plants, red	F_2	89	26	33		148	9:3:4	.60
40548 = 37079-18 x 38201-4	F_1	22				22		
Three plants, deep pink	F_2	119	38	22	29	208	9:3:4**	.65
40550 = 37079-18 x 37078-11	F_1	25				25		
Three plants, deep pink	F_2	73	27	9	31	140	9:3:4**	.45

* In the field this plant was pure white but under favorable conditions in the greenhouse the petals would show an occasional flush of anthocyanin.
** The white and white-flushed were added.

TABLE XVIII

PARENTAGE	GENERATION	PROGENY	TOTAL
PINK MATCHLESS, deep pink	P_1	None	
WOBURN, crimson	P_1	163 self-colored, 39 white-variegated, 58 transition color	260
34535 = WOB. X P. MATCH.	F_1	7 self-colored, 2 white variegated, 3 transition color	12
34535-2, purple	F_2	148 self-colored, 44 white-variegated, 49 transition color	241
34535-4, white var. purple	F_2	18 white var. purp. or crim., 4 wh. var. red or pink, 11 wh.	33
34535-4-6, white var. deep pink	F_3	47 white var. d. p., all with picotee pattern, 7 white	54
34535-4-12, white var. crimson	F_3	72 white var. crimson, all with picotee pattern	77

purple, 4 deep pink, 3 maroon-broadly-variegated-purple, 1 pale lilac-variegated-purple, and 1 white-variegated-pink. It is from the pale lilac-variegated-purple (Table XVIII) that all the lines with this pattern on whitish ground have been derived.

This pattern occurs in all variations of intensity from the faintest suggestion to the deeply colored shown in fig. 1, pl. 10. When the pattern is strong either in extension or intensity of color, the background also becomes lightly colored. That is, if the pattern is red or deep pink the otherwise white ground becomes faintly colored pink, and if the pattern is crimson or purple the ground becomes pale lilac. Under field conditions this ground color often bleaches to white but in the greenhouse it usually remains. On clear yellow ground the pattern is very faint, often limited to a pale edge at the distal ends of the petals. The same pattern occurs in the transition series (fig. 3, plate 10), but here it appears to be made up of broader stripes and blotches than when it occurs on whitish ground. Because most of the plants with this pattern have also had stripes typical of either the t^{var} or a^{var} variegations, it was thought that perhaps this pattern was only expressed in t^{var} and a^{var} genotypes and that the apparently "pure" picotee pattern

TABLE XIX

PARENTAGE	GENERATION	PROGENY			TOTAL	RATIO	P
		Self-color	White var.	White and flushed			
40534 = 34535-4-12-1 x 37030-6	F_1	26 cr.			26		
Two plants, crimson	F_2	127	45	80	252	9:3:4	.04
40535 = 37030-6 x 34535-4-12-2	F_1	21 cr.			21		
Two plants, crimson	F_2	73	27	41	141	9:3:4	.45
40546 = 37079-18 x 34535-4-12-1	F_1	24 purp.			24		
Four plants, purple	F_2	154	57	95	306	9:3:4	.04
40580 = 34535-4-12-1 x 37079-29	F_1	26 purp.			26		
Two plants, purple	F_2	93	37	39	169	9:3:4	.50
40581 = 34535-4-12-2 x 37079-29	F_1	29 purp.			29		
Two plants, purple	F_2	97	41	47	185	9:3:4	.50

in reality was due to a relatively "low" allele of i^{var} or a^{var}, with a "high" allele of the gene determining the picotee pattern.

In Table XIX is summarized the data from crosses between picotee pattern and *y*-whites. It is apparent that, with the exception of the crosses 40534 and 40546, the segregation from full self-color is the same as if the genes in question were y^{fl} and a^{var}. The results from the crosses 40534 and 40546 do not agree too well with the hypothesis but it was noted that the self-colored and white-flushed plants from these crosses were, on the average, much more vigorous than the variegated plants. The reason for this difference in vigor is not known. Among the variegated individuals there were some that appeared to be *picotee* only, others that were *random narrow*, while the majority showed both types of variegation. If one considers those that appeared to have only random narrow variegation against the remainder, the proportions for the five crosses are: 7:38, 6:21, 10:47, 8:29 and 10:31, or 41:166 for all of them, which is approximately $\frac{1}{5}$ of the total.

The F_1 plants of each of the crosses between picotee pattern and random narrow variegation showed both types of variegation (Table XX). In the F_2 generation there was segregation for both patterns. Since a heavy picotee pattern might mask the stripes of the other variegation pattern, it is safer to consider those having only random narrow variegation. By so doing it becomes evident that in four of the six crosses this variegation occurred in about $\frac{1}{4}$ of the total number of plants. On the other hand, in the other crosses (40538 and 40540), only one plant of the four that were selfed segregated for random variegation. The plant 37078-11 that was used as one parent in these crosses came from a line in which weak picotee patterns had been observed and, although this plant had been classified as having random variegation only, it is possible that it also had a weak picotee pattern. It was not possible to check on this as the plant was no longer available when the difference among these crosses became apparent.

A white-flowered plant (39024-26) obtained from a lavender line segregating for white (40 lavender:11 white) was crossed to a pure-breeding white whose genotype had been determined to be *Y I a S r m*. The result was 15 F_1 plants, all of which were variegated crimson on white ground, 3 with random narrow variegation, and 12 with both random and picotee patterns. Two F_1 plants that plainly showed both types of variegation were selfed. In the F_2 generation of 96 plants, 60 were variegated while 36 were white. Of the 60 variegated plants, 12 were classified as having picotee pattern, 18 random variegation, and 30 with both random and picotee. The proportion of 60 variegated to 36 non-variegated suggests a 9:7 ratio or segregation for two genes probably *y* and *a*. If this is correct the white extracted from the lavender line must have been of the genotype $y\,I\,a^{var}$ so that the F_1 plants were $\frac{Y}{y}\frac{I}{I}\frac{a^{var}}{a}$. This genotype would account for the segregation of variegated and white in approximately 9:7 proportions. The ratio between all the plants showing the picotee and those with the random type variegation is 42 to 18, suggesting that the F_1 plants were heterozygous for a dominant gene capable of producing the picotee pattern only in the presence of

TABLE XX

PARENTAGE	GENERATION	PROGENY						TOTAL
		White var. crimson			White var. red			
		pic.	p + r	rand.	pic.	p + r	rand.	
40537 = 37030-16* x 34535-4-12-2**	F_1		25					25
40537-11	F_2	20	26	10	1	13	6	76
40537-16	F_2		58	18		16	13	105
40538 = 37030-16 x 34535-4-12-3	F_1		10					10
40538-2	F_2	18	18	12	3	4	15	70
40538-4	F_2	17	22	7	1	12	5	64
40540 = 37078-11 x 34535-4-12-1	F_1		13					13
40540-6	F_2	57	5		1	8		71
40540-9	F_2	10	8	12	1	6	3	40
40542 = 37078-11 x 34535-4-12-1	F_1		11					11
40542-8	F_2	26	26		3	6		61
40542-10	F_2	15	12		1	14		42
40577 = 34518-1-14*** x 34535-4-12-1	F_1		26					26
40577-9	F_2	7	10	5		3	2	27
40577-19	F_2	20	10	5	2	7	2	46
40578 = 34518-1-14 x 34535-4-12-2	F_1		21					21
40578-2	F_2	1	22	8		5	4	40
40578-8	F_2	2	27	6	1	8	5	49

* For P_1 data on 37030-16 and 37078-11 see Table XVII.
** For P_1 data on 34535-4-12-1, 12 and 13 see Table XVIII.
*** For P_1 data on 34518-1-14 see Table VIII.

another variegation gene, in this case a^{var}.

When a plant having flowers that were orange variegated with red picotee pattern was crossed to a white-variegated-red of the random narrow type, the F_1 of 21 plants consisted of 11 red self-colored plants and 10 with white flowers variegated red with both random and picotee patterns. No F_2 generation has yet been grown from this cross.

Much more work is needed before the exact inheritance of the picotee pattern will be known. The best hypothesis that can be made at this time is that it is determined by a dominant gene non-allelic with the other variegation genes discussed and capable of producing its characteristic pattern only in the presence of either i^{var} or a^{var}. For purposes of identification this gene will be designated *Pic*.

d. Salmon-Red Variegation.—

This type of variegation was first found on salmon ground but has since occurred on every member of the *s* series, that is, *salmon*, *light pink*, and *lavender*. It is the most erratic of the different types of variegation encountered in this study. Red variegation on salmon ground is the only color that has been studied for the inheritance of this feature, all the data pertaining to this variegation in other colors having been derived incidentally from crosses made for other purposes. The

origin of this type of variegation, as far as this study is concerned, can be traced to the commercial variety SPECTRUM. This variety has been found in these studies to be heterozygous for yellow and salmon. Thus the genotype is $\frac{Y\ I\ A\ S\ r\ m}{Y\ i\ A\ s\ r\ m}$. It is of a rather dull red color. During the 20 years that it has been widely grown, it has produced at least one mutation toward a deeper, more attractive red which has largely replaced the parent variety. It is known in the trade as SPECTRUM SUPREME. A salmon mutant, also widely grown commercially and known as SALMON SPECTRUM, has occurred several times. This salmon mutant in turn frequently mutates back to red, but most of these mutations are limited to a few red stripes or sectors of individual flowers only rarely involving whole flowers. Other commercial salmon-colored varieties known to be genetically related to SPECTRUM, such as CHARM, LADDIE and SURPRISE, frequently mutate to red in the same manner (pl. 10, figs. 5, 6).

TABLE XXI

PARENTAGE	GENERATION	PROGENY				TOTAL	RATIO	P
		Deep pink	Red	Salmon var. red	Salmon			
PINK ABUNDANCE, deep pink	No P_1							
SPECTRUM, red	No P_1							
SURPRISE, salmon	No P_1							
34520-6-13	P_1		40			40		
33503 = SURPRISE x SPECTRUM	P_1		6		4	10	1:1	
33503-2, salmon	F_2				23	23		
33514 = PINK ABUND. x SPECTRUM	F_1	13	11	6		30	3:1*	
33514-20, salmon var. red	F_2			9	3	12	3:1	
34509 = 33514 x 33503-2	F_1		6	8		14	1:1	
34509-3, salmon var. red	F_2		5	66	37	108	?	
34509-5, salmon var. red	F_2			38	11	49	3:1	.65
34509-10, salmon var. red	F_2			30	12	42	3:1	.60
34509-12, salmon var. red	F_2			27	24	51	3:1	**
34509-11, red	F_2		32		14	46	3:1	.40
34509-14, red	F_2		34		9	43	3:1	.50
34509-10-1, salmon var. red	F_2			16	8	24	3:1	.40
34509-10-1-1, salmon var. red	F_4			1	27	28		
34509-10-1-2, salmon var. red	F_4		1	36	3	40	?	
34509-10-1-2 x 34520-6-13	F_1		27			27		
Plant #1	F_2		37	9		46	3:1	.40
Plant #2	F_2		43	8	1	52	3:1	.20
Plant #3	F_2		35	16	2	53	3:1	.15
Salmon from #2	F_3			37	14	51	3:1	.65
Salmon from #3	F_3		1	27	11	39	3:1	.60

* The ratio is based on self-color versus variegated.
** Less than .01.

In Table XXI are shown the crosses of particular interest in connection with this type of variegation. The cross 34509 indicates that this variegation is a simple recessive to full self-color. The other crosses show that such is the case. On the other hand, nearly all the salmon-variegated-red plants that have been selfed have given more salmon selfs than was expected on the basis of a single gene difference. However, some salmon plants extracted from such progenies in the next generation produced again a majority of salmon-variegated-red plants, as if they in reality had been salmon-variegated-red. This irregular behavior and the fact that most of the spontaneous occurrences of this type of variegation have been limited to a few stripes or sectors involving only one or two petals indicate that such variegation is due to some instability of the *s* gene or to some other gene capable of causing the *s* allele to mutate to S. That it is the *s* gene which mutates is evident by the variegation being limited to the *s*-series. In order to identify this gene for further studies it will be designated s^{var}. There is no evidence that the gene for picotee pattern, discussed in the preceding section, has any effect on this gene.

Discussion

As far as we are aware, the only previous published data on the inheritance of flower color in the carnation, aside from the preliminary report by the senior author in 1939, is that of Connors ('14). From the results of a cross between a commercial white and a commercial yellow carnation, he concluded that white was dominant to yellow and red, and yellow in turn to red. Our results show that he was right in concluding that white is dominant to yellow (actually epistatic) but not as to white and yellow being dominant to red or pink. The appearance of red or pink stripes on white or yellow flowers from selfing what was supposed to be pure whites, in all probability, was due to mis-classification of the F_1 plants. In fact, Connors himself stated that at the end of the season the yellow parent, JAMES WHITCOMB RILEY, produced some flowers that were streaked with red. That places this parent in the variegated class. The white parent, WHITE PERFECTION, must have been homozygous for *a*, as otherwise the F_1 generation would have been anthocyanin self-colored. One of the parents must have been heterozygous for *y*, as otherwise no pale yellow or cream-colored individuals would have occurred in the F_2 generation. If one assumes that the yellow parent was homozygous for a^{var} the results are entirely compatible with the genotypes suggested by this study. The whites obtained in the F_1 were probably lightly variegated but grown under conditions unfavorable for the production of this variegation. Under field conditions in California it was found necessary to check the populations suspected of variegations several times during the year to be reasonably certain that plants classified as whites were actually white.

The genotypes suggested here are in many respects similar to those suggested for other plants. As Wheldale found in *Antirrhinum majus* ('10), Lawrence and Scott-Moncrieff in *Dahlia variabilis* ('35), and Buxton in *Primula acaulis* ('32), two genes are concerned with the production of the anthoxanthins in the carna-

TABLE XXII

PARENTAGE	GENERATION	PROGENY										TOTAL	RATIO	P
		Deep pink	Light pink var. d. pink	Light pink	Red	Salmon var. red	Salmon	White var. pink	White	Yellow var. red or pink	Pale yellow and yellow			
MAINE SUNSHINE, yellow	P_1										63 yel. 15 p.y.	78	3:1	.20
37109-1, white	P_1								23			23		
34520-17-35, salmon	P_1						26				10	36	3:1	.10
34520-17-35-2, salmon	P_1						28					28		
39571 = 34520-17-35-2 x 37109-1	F_1	1	4	1	1	7	2					16		
Two plants, salmon	F_2						95		74			169	9:7*	.99
Two plants, salmon var. red	F_2				2	45	35	14	48			143	9:7	.85
One plant, light pink	F_2			34			12		42			88	9:7	.45
Two plants light pink var. deep pink	F_2		51	47				4	58			160	9:7	.20
38629 = M. S. x 34520-17-35	F_1		4	19						15		38		
Two plants, yellow var.	F_2									30	39	69		
One plant, light pink	F_2			81				17	14	19	13	144	9:3:4:**	.60
One plant, light pink	F_2			56				4	38	10	20	128	27:21:16	.90
One plant, light pink var. deep pink	F_2		29	29				5	43	7	23	136	27:21:16	.65
38638 = 34520-17-35-35 x M. S.	F_1		1	4						10		15		
Two plants, yellow var.	F_2									19	47	66		
One plant, light pink	F_2			80				18	8	27	6	139	9:3:4	.90
One plant, light pink var. deep pink	F_2		23	14				7	24	10	5	83	27:21:16	.50

* The ratios for the cross 39571 are based on A-color versus white.
** The ratios for the crosses 38629 and 38638 are based on A-color: white: transition color.

tion, *Y* with yellow and *I* with ivory (white). As in *Antirrhinum*, *I* is epistatic to *Y*, but plants with the allele *y* are white only in combination with *I*. In combination with the recessive allele *i* they are of a pale yellow which in strong sunlight may bleach to cream. As in *Antirrhinum majus*, *Primula acaulis*, *Tropaeolum majus* (Scott-Moncrieff, '36), and *Pharbitis nil* (Hagiwara, '32), only one gene *A* is concerned with general anthocyanin production. Plants homozygous for *a* in the presence of *I* are pure white, as is also *y I a*. Plants with *y I A* usually have colored anthers, tips of stigmas, leaf bases and nodes and, under favorable conditions, a trace of anthocyanin in the petals. The gene S determines the concentration of the anthocyanin, permitting full intensity, while in the presence of its recessive allele a much smaller amount of anthocyanin is formed, resulting in a series of pale colors. One, perhaps two, as yet unidentified dominant genes further suppress the amount of anthocyanin. As in the China Aster (*Callistemma chinensis* (L.) Skeels) studied by Wit ('37), the gene *M* controls the glycosidic type of the anthocyanin. In all genotypes with *M* the number of sugar molecules attached to the anthocyanidin molecule is two, in genotypes with *m*, only one.

TABLE XXIII

SUMMARY OF GENOTYPES AND PHENOTYPES FOR SELF-COLORED CARNATIONS

Genotypes	Phenotypes
Y I A S R M =	Magenta-purple
Y I A S R m =	Crimson
Y I A S r M =	Deep pink
Y I A s R M =	Lavender
Y I A S r m =	Scarlet, red
Y I A s R m =	Lavender*
Y I A s r M =	Light pink
Y I A s r m =	Salmon
y I A – – –** =	White petals, anthocyanin-colored anthers and stigmas***
Y I a – – – =	Pure white petals, white anthers and stigmas
y I a – – – =	Pure white petals, white anthers and stigmas
Y i A S R M =	Maroon
Y i A S R m =	Maroon
Y i A S r M =	Orange
Y i A s R M =	Pale maroon
Y i A S r m =	Orange
Y i A s R m =	Pale maroon
Y i A s r M =	Salmon-yellow
Y i A s r m =	Salmon-yellow
Y i a – – –** =	Yellow
y i A – – – =	Pale yellow
y i a – – – =	Pale yellow

* This lavender cannot be distinguished from *M* lavender except by breeding tests. The same is true for maroon, pale maroon, and orange.

** Any allele of S R M may be substituted for––– without change in appearance.

*** Under favorable conditions the petals also may be faintly flushed with anthocyanin. The kind of anthocyanin will depend on the specific genotype but only the pink-red series with *r* and the crimson-magenta series with *R* can be recognized by inspection. Whether the plants have *m* or *M* cannot be determined with certainty by inspection.

Also, as in Aster, the gene *R* determines the kind of anthocyanin. In genotypes with *R* the product is cyanin, whereas with *r* it is pelargonin only.

The inheritance of flower variegation in the carnation needs further study. The more or less continual outcropping of variegated individuals in crosses made to study self-colors was at times quite a nuisance, but now that the main genes for the self-colors are established and the connection between them and the genes for variegation are at least partly known it will be easier to plan the required critical crosses necessary to complete the picture. All of the genotypes possible with the genes identified so far are listed in Tables XXIII and XXIV.

It is of interest that all of the flower color genes identified in this study apparently also are concerned with the general vigor of the plants. The recessive types have been, on the average, less vigorous than the corresponding dominants and the multiple recessives definitely weaker than the multiple dominants.

The genes *I* and *M* are of particular interest in this connection. Plants with *i* (that is, yellows) and members of the transition series are usually quite deficient in the cuticular waxy material responsible for the bloom or glaucousness of the leaves and stems. Plants with i^{var} are generally somewhat better in this respect but still deficient. This deficiency seems to be of relatively little consequence in the greenhouse but out-of-doors, especially in hot and dry weather, the plants are much harder to grow. Probably this deficiency in cuticular wax means less protection against excessive transpiration.

By selection it has been possible to obtain *i* plants with so much more glaucousness that they are indistinguishable from *I* plants in the greenhouse and do very well under most field conditions. However, all these plants also have *M*. Every selection made among *i m* plants has been definitely inferior to the best selections from the *i M* group. It would appear therefore that the dominant allele of *M*, or genes associated with it, can in part make up the deficiency in glaucousness caused by *i*.

TABLE XXIV

SUMMARY OF GENOTYPES AND PHENOTYPES FOR VARIEGATED CARNATIONS

IVa. Random Narrow Variegation	
Y I a^{var} S *R M* =	White with narrow stripes of purple
Y I a^{var} S *R m* =	" " " " " crimson
Y I a^{var} S *r M* =	" " " " " deep pink
Y I a^{var} *s R M* =	" " " " " lavender
Y I a^{var} S *r m* =	" " " " " red
Y I a^{var} *s R m* =	" " " " " lavender
Y I a^{var} *s r M* =	" " " " " light pink
Y I a^{var} *s r m* =	" " " " " salmon
y I a^{var} – – – =	White
Y i a^{var} S *R M* =	Yellow with narrow stripes of purple
Y i a^{var} S *R m* =	" " " " " crimson
Y i a^{var} S *r M* =	" " " " " deep pink
Y i a^{var} *s R M* =	" " " " " lavender
Y i a^{var} S *r m* =	" " " " " red
Y i a^{var} *s R m* =	" " " " " lavender
Y i a^{var} *s r M* =	" " " " " light pink
Y i a^{var} *s r m* =	" " " " " salmon
y i a^{var} – – – =	Pale yellow

IVb. Random Broad Variegation

Y i^{var} *A S R M*	=	Maroon with broad stripes of purple
Y i^{var} *A S R m*	=	" " " " " crimson
Y i^{var} *A S r M*	=	Orange with broad stripes of deep pink
Y i^{var} *A s R M*	=	Pale maroon with broad stripes of lavender
Y i^{var} *A S r m*	=	Orange with broad stripes of red
Y i^{var} *A s R m*	=	Pale maroon with broad stripes of lavender
Y i^{var} *A s r M*	=	Salmon-yellow with faint broad stripes of pink
Y i^{var} *A s r m*	=	Salmon-yellow with faint broad stripes of pink
Y i^{var} *a – – –*	=	Yellow with broad stripes of white
y i^{var} *A – – –*	=	Pale yellow
y i^{var} *a – – –*	=	Pale yellow

IVc. Picotee Pattern—This pattern can presumably be superimposed on any *i*$^{var.}$ or *a*$^{var.}$ genotype by the gene *Pic*.

IVd. Salmon-Red Variegation

Y I A s^{var} *R M*	=	Lavender with purple stripes
Y I A s^{var} *R m*	=	Lavender with crimson stripes
Y I A s^{var} *r M*	=	Light pink with deep pink stripes
Y I A s^{var} *r m*	=	Salmon with red stripes

IVe. Flushed Variegation

yfl I A S R M	=	White flushed magenta-purple
yfl I A S R m	=	" " crimson
yfl I A S r M	=	" " deep pink
yfl I A s R M	=	" " lavender
yfl I A S r m	=	" " red
yfl I A s R m	=	" " lavender
yfl I A s r M	=	" " light pink
yfl I A s r m	=	" " salmon*
yfl I a – – –	=	White
yfl i A – – –	=	Pale yellow flushed deep yellow to orange
yfl i a – – –	=	Pale yellow

Mixed types of Variegation

Y i^{var} *a*^{var} *– – –*	=	Yellow with broad stripes of white and narrow stripes of any anthocyanin color depending on specific genotype.
yfl I a^{var} *– – –*	=	White, or white flushed with anthocyanin, depending upon relative "strength" of the alleles.
yfl i^{var} *A – – –*	=	Not known.

* The "flushed" phenotypes, lavender, light pink, and salmon, cannot be distinguished except by breeding tests.

SUMMARY

Six independent genes for self-colors in the carnation have been identified. Their functions may be summarized as follows:

Y controls the production of yellow anthoxanthin. It is hypostatic to *I*. In the presence of the recessive allele *y*, only a limited amount of anthoxanthin is developed, resulting in pale yellow or cream-colored flowers.

I controls the production of ivory-white anthoxanthin. It is epistatic to *Y*. The recessive allele *i* permits the production of yellow anthoxanthin.

A is the basic gene for anthocyanin. It is fully effective only in combination with *Y* and *I*. In combination with *i* only a small amount of anthocyanin

is produced, resulting in a series of pale colors on yellow background (the transition series). In the presence of the recessive allele *a* no anthocyanin is produced. The interrelationship of these three genes is shown by the following genotypes:

27 *Y I A* = full anthocyanin self-color.
9 *y I A* = white or near white.
9 *Y I a* = pure white.
3 *y I a* = pure white.
9 *Y i A* = transition colors (small amount of anthocyanin on yellow background).
3 *Y i a* = yellow.
3 *y i A* = pale yellow.
1 *y i a* = pale yellow.

S controls the amount of anthocyanin. In the presence of its recessive allele *s* much less anthocyanin is formed. One, possibly two, as yet unidentified genes modify the effect of S-*s*.

R determines the kind of anthocyanin. The dominant allele causes the production of cyanin resulting in crimson or dark red flowers, whereas its recessive allele *r* causes the production of pelargonin only, resulting in bright red or scarlet flowers.

M determines the number of sugar molecules attached to the anthocyanin molecule. With the dominant allele there are two sugar molecules attached whereas in the presence of the recessive allele *m* only one sugar molecule occurs.

The number of sugar molecules attached to the anthocyanin has a marked effect on the anthocyanin. For instance, *M* with *r* changes the color from bright red or scarlet to deep pink and *M* with *R* changes crimson or dark red to magenta-purple. In general, it may be said that the addition of the second sugar molecule has a bluing effect on the anthocyanin color. It has no visible effect on the anthoxanthin.

At least five genes are concerned with the different types of flower variegation in the carnation. Four of these appear to be multiple alleles with genes for self-color. They are:

y^{fl} causes limited amounts of anthocyanin to be produced under favorable conditions. This anthocyanin occurs as a tinge or flush on white background. This type has been termed *flushed*.

i^{var} with *a* causes broad, indefinite, randomly distributed stripes of ivory anthoxanthin on yellow ground, and with *A* similar stripes of anthocyanin on colors of the transition series. This variegation has been termed *random broad*.

a^{var} causes narrow, definite, randomly distributed stripes on white or yellow background. This variegation has been termed *random narrow*.

s^{var} causes sporadic, irregular striping on any member of the *s* series (salmon, light pink, lavender).

Pic causes a definite variegation pattern, *picotee*, in the presence of I^{var} or a^{var}. The recessive allele *pic* probably has no visible effect.

The results indicate that more multiple alleles of these genes concerned with flower variegation exist, or that their action is influenced by modifying genes.

All of the genes for flower color appear to be concerned also with the general vigor of the plants, for the recessives were, on the average, somewhat less vigorous than the corresponding dominants, and multiple recessives were definitely weaker than the multiple dominants.

The gene *I* seems also to be directly involved in the development of the cuticular waxy material responsible for the "bloom" or glaucousness of the leaves and stems, as plants with *i* are quite deficient in this respect. The gene *M* or genes associated with it appears to be able partly to make up this deficiency caused by *i*.

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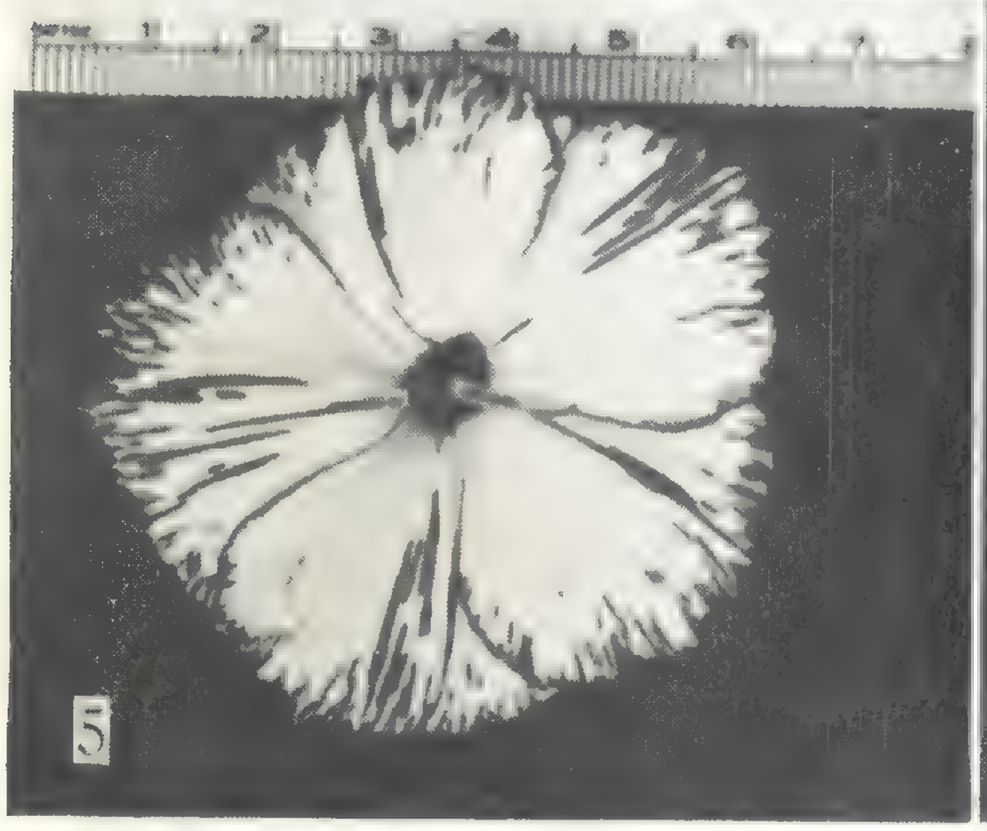
Explanation of Plate

PLATE 9

Dianthus caryophyllus

Fig. 1. Pure white.
Fig. 2. White flushed red toward center.
Fig. 3. Flushed red toward edges.
Fig. 4. Evenly flushed.
Figs. 5 & 6. *Random narrow* variegation.



MEHLQUIST & GEISSMAN—INHERITANCE IN THE CARNATION

Explanation of Plate

PLATE 10

Dianthus caryophyllus

Fig. 1. Strong crimson *picotee* pattern on white background.
Fig. 2. Light *picotee* pattern with some *random narrow* stripes.
Fig. 3. Strong red *picotee* pattern on orange background.
Fig. 4. *Random broad* red stripes on orange background.
Fig. 5. *Salmon-red* variegation in left third of salmon flower (CHARM).
Fig. 6. Individual petals from flower in fig. 5.

MEHLQUIST & GEISSMAN—INHERITANCE IN THE CARNATION

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THE EFFECT OF THE MEDIUM ON APPARENT VITAMIN-SYNTHESIZING DEFICIENCIES OF MICROORGANISMS[1]

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Beadle and Tatum's work ('45) on biochemical mutants of *Neurospora* has resulted in wide acceptance of the view that it is relatively easy to distinguish strains genetically capable from those genetically incapable of synthesizing vitamins. They discovered many mutants apparently incapable of performing specific syntheses. The present paper reveals, however, that different synthetic media so affect the growth of organisms that conclusive demonstration of specific deficiency requires a much more critical study of the environment than has hitherto been achieved. Differential growth of cultures in a synthetic medium which deviates in many respects from the natural substrate may prove very useful for genetical diagnosis but may not give reliable information concerning the synthetic activity of the organism under normal conditions. Without critical testing it is difficult to say whether a given deficiency is absolute. The following data will show that the standard test of ability to grow in the presence and inability to grow in the absence of a given vitamin in a synthetic medium is inadequate and that the criterion of equal increments of growth for equal additions of the vitamin may give an ambiguous answer.

A COMPARISON OF TWO SYNTHETIC MEDIA

Table I shows the formulas of the synthetic media used by Burkholder ('43), Hutner (unpublished), Wickerham ('46), and Beadle and Tatum ('45). Many experiments have shown that Hutner's medium is a very different substrate for yeast growth from Burkholder's. This was clearly revealed by growing cultures Nos. 3 and 10 (Table II) on two batches of each medium, one to which no pantothenate was added and the other containing 50 γ of pantothenate per liter (fig. 1). Culture No. 3 does not begin to grow in Burkholder's medium without

[1]This work was supported by grants from Anheuser-Busch, Inc., The American Cancer Society, and Washington University.

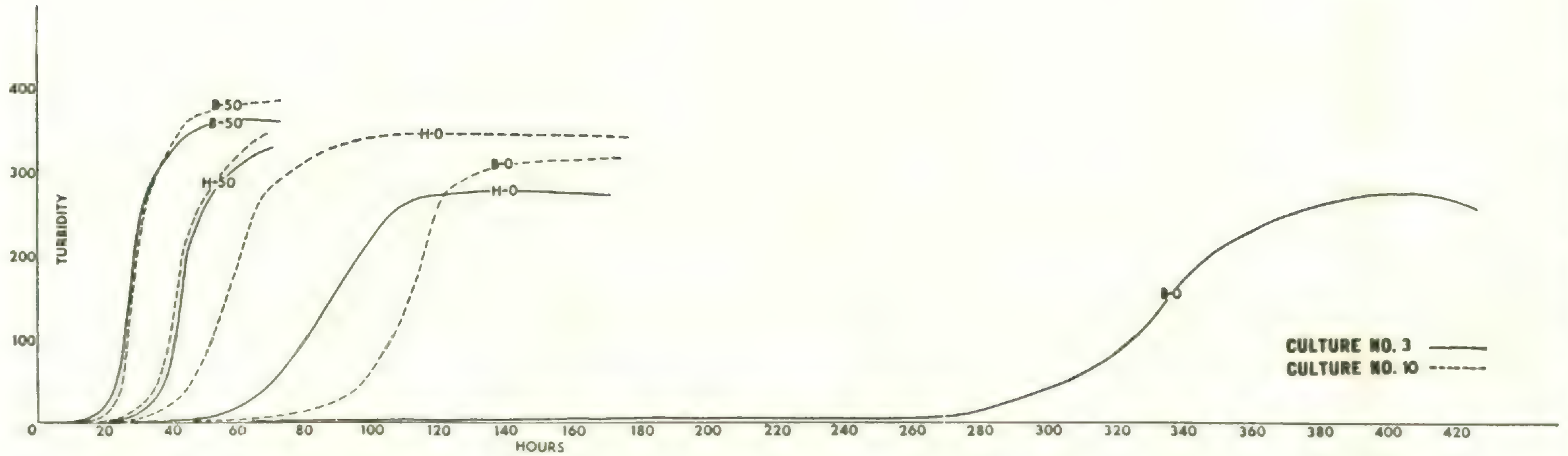

Fig. 1. Comparison of the amounts of growth on Burkholder's and Hutner's media. The turbidity indicated by a Klett Photoelectric Colorimeter is plotted against the time in hours after inoculation. Culture No. 3 was grown on two batches of Hutner's medium, one containing 50 γ of pantothenate per liter and the other containing no added pantothenate. It was also grown on two different batches of Burkholder's medium, one containing 50 γ per liter of pantothenate and one no added pantothenate. Culture No. 10 was also grown on these four different kinds of media.

added pantothenate until after 200 hours, but growth is completed in Burkholder's medium containing 50γ of pantothenate per liter after 50 hours. Readings taken at 72 hours would be interpreted to mean that it was a "nonsynthesizer." Culture No. 10 is capable of more rapid growth than culture No. 3 in Burkholder's without added pantothenate and it grows much more slowly in the absence of pantothenate than in its presence. Moreover, it synthesizes pantothenate after a considerable lag in Burkholder's medium; in Hutner's medium the lag is much shorter. Burkholder's medium is a much better diagnostic medium than Hutner's since growth occurs more rapidly on it than on Hutner's when pantothenate is supplied, but when pantothenate is not added, growth occurs less rapidly on Burkholder's than on Hutner's. That is, Burkholder's is a better medium when pantothenate is added but a poorer medium without added pantothenate.

THE "VITAMIN" PEDIGREE

Pedigree I (Table II) describes the melibiose-fermenting capacity of the various cultures which were subsequently investigated in some detail for their "vitamin-synthesizing" activity on Burkholder's medium according to his technique. The original diploid culture of S. *cerevisiae* (No. 1) was incapable of fermenting melibiose, and its offspring, cultures Nos. 3, 4, 5, and 6, were similarly incapable. In this pedigree numbers are used to indicate the different cultures, and each group of four in a single column includes the cultures produced by the four spores of a single ascus. Thus cultures 3, 4, 5, and 6 were originally from one diploid ascus of S. *cerevisiae*. Culture No. 2 *(S. carlsbergensis)* fermented melibiose, as did all of its haploid progeny. Culture No. 7 was the only survivor of a single ascus, and a mating between it and No. 4 produced a hybrid supposedly heterozygous for the ability to ferment melibiose.

This pedigree involves a non-Mendelian phenomenon which will be considered in greater detail in a later paper (Lindegren & Lindegren, '47). The pedigree is merely presented here for subsequent reference in tracing the descent of the different cultures.

HYBRIDS BETWEEN YEASTS SUPPOSEDLY DIFFERENT IN VITAMIN-SYNTHESIZING ABILITY

The members of this pedigree were characterized (Lindegren and Lindegren, '45) as "vitamin-synthesizers" and "vitamin-nonsynthesizers." The distinction between ability and inability to synthesize was made by Burkholder's method with his medium. This procedure defines readings taken at 72 hours as diagnostic. We have since discovered that this method does not give conclusive results, for if growth were allowed to continue, the supposedly nonsynthesizing yeasts will eventually begin to grow and will finally, in most cases, attain a level equal to that of the so-called synthesizers. However, at the end of 72 hours a 10- or 20-fold difference in growth often exists as indicated by reading the turbidity with a Klett Photoelectric Colorimeter. Haploids of S. *carlsbergensis* were characterized

TABLE I
FORMULAS OF DIFFERENT SYNTHETIC MEDIA

	Burkholder's	Hutner's	Beadle & Tatum's	Wickerham's
	Grams per liter			
Dextrose	20.0	20.0		10.0
Sucrose			20.0	
Recrystallized asparagine	2.0			1.0*
K_2HPO_4				0.125
KH_2PO_4	1.5	1.0	1.0	0.875
$MgSO_4.7H_2O$	0.5	0.2	0.5	0.5
$CaCl_2.2H_2O$	0.33	0.037	0.1	0.1
$(NH_4)_2SO_4$	2.0			1.0*
KI	0.0001			0.0001
NaCl			0.1	0.1
Sodium citrate		0.8		
Citric acid		0.2		
$(NH_4)_2HPO_4$		0.8		
Ammonium tartrate			5.0	
$(NH_4)NO_3$			1.0	
	Parts per million			
Boron	0.01		0.01	0.01
Manganese	0.01	0.5	0.02	
Zinc	0.07	4.0	2.00	0.07
Copper	0.01	0.1	0.10	0.01
Molybdenum	0.01		0.02	
Iron	0.05	4.0	0.20	0.05
	Micrograms per liter			
Thiamin	200	200		400
Pyridoxine	200	200		400
Nicotinic acid	200	200		400
Pantothenate	200	200		400
Biotin	2	2	5.0	2
Inositol	10,000	10,000		2,000
Riboflavin				200
p-amino-benzoic acid				200
	pH 5.0 with NaOH	pH 6.0 with citric acid		pH 5.3

* Either asparagine or $(NH_4)_2SO_4$ was used.

as biotin +, pantothenate +, and pyridoxine —; haploids of *S. cerevisiae* were characterized as biotin —, pantothenate —, and pyridoxine +, according to Burkholder's technique.

Table III shows the Klett readings obtained after 72 hours by Burkholder's technique of these different cultures. It appears that culture No. 4 is a non-synthesizer of pantothenate, while No. 7 is a synthesizer. A hybrid between No. 4

TABLE II

PEDIGREE OF A HYBRID BETWEEN *S. CEREVISIAE* (LK) AND *S. CARLSBERGENSIS* (MRAK, 126)

1		S. *cerevisiae* me diploid (Lk)			2		S. *carlsbergensis* Me diploid (Mrak, 126)						
3	a	me			7	α	Me		74	Me			
4	a	me			76		Me		80	Me			
5	α	me			77		Me		81	Me			
6	α	me			78		Me		82	Me			
					79		Me		83	Me			
4 × 7 (a me × α Me)													
			10 diploid										
20	α	Me	12	Me	16	Me	35	Me	90	Me	94	Me	110	Me
21	α	Me	13	Me	17	Me	36	Me	91	me	95	Me	111	me
22	a	Me	14	Me	18	Me	37	me	92	Me	96	Me	112	Me
23	a	Me	15	Me	19	Me	38	Me	93	Me				
4 × 20 (a me × α Me)														
			25	Me	29	Me	33	Me	39	me				
			26	Me	30	me	34	me	40					
			27	me	31	Me	35	Me	41	Me				
			28	me	32		36	me	42	me				
5 × 23 (α me × a Me)														
45		Me	49	Me	53	me	57	Me	61		65		69	me	86	Me
46			50	me	54	me	58	me	62		66	me	70	Me	87	Me
47		me	51		55	Me	59	Me	63	me	67		71	Me	88	me
48		me	52		56		60	me	64	Me	68	Me	72	me	89	me
20 × 23 (α Me × a Me)																
124		Me	128	Me	136	Me	140	Me	144	Me	150					
125		me	129	Me	137	Me	141	me	145	Me	151	Me				
126		me	130	Me	138	Me	142	Me	146	Me	152	Me				
127			131	Me	139	Me	143	Me			153	Me				
4 × 49 (a me × α Me)							4 × 55 (a me × α Me)							
			104	Me					117	me	121			
			105	me					118	Me	122			
			106	me					119		123			
									120	Me				
5 × 72 (α me × a me)							7 × 72 (α Me × a me)							
98		me	101	me					Me		me			
99		me	102	me					Me		Me			
100		me	103	me					Me		Me			
									Me					

and No. 7 (culture No. 10) appears capable of synthesizing pantothenate, but the four haploid progeny, Nos. 20, 21, 22, 23, do not reveal any segregation for this character according to this specific criterion. (The pantothenate character does segregate according to Mendelian ratios in other pedigrees which do normally segregate regularly.) It was subsequently discovered that none of these cultures was a nonsynthesizer and that the data appearing in Table III do not give an adequate picture of the synthetic ability of the organisms. The inadequacy of this characterization will be dealt with in detail below.

VITAMIN-SYNTHESIZING ABILITY OF SUPPOSEDLY DEFICIENT YEASTS IN A NATURAL MEDIUM

Dr. F. W. Tanner, Jr. (unpublished) grew various members of pedigree I (Table II) in a natural medium containing molasses and corn-steep liquor for 72 hours. When the yeast and the medium were assayed it was found that under these conditions all the cultures synthesized similar amounts of the different vitamins. Apparently the cultures were not clearly differentiated by ability and inability to synthesize the vitamins, but were all capable of synthesis under favorable conditions.

CONTINUOUS OBSERVATION OF GROWTH

Our present technique, an example of which has been presented in fig. 1, requires a much longer observation period. Many of the same cultures were reinvestigated and were sometimes observed for as long as a month, readings being made over the entire period. This is quite different from the standard practice of discontinuing the experiment after 72 hours. If the period of observation was extended for a longer time, haploid cultures of S. *cerevisiae* (as well as of S. *carlsbergensis*) were found to be able to grow on Burkholder's medium in the absence of pantothenate. This was equally true of all the progeny of the hybrid, many of which had previously been described as "nonsynthesizers." In some cases there was a delay of more than 600 hours before growth began. We grew the cultures in 6 x ¾-inch Kimble tubes and determined the amount of growth by measuring turbidity on the Klett Photoelectric Colorimeter adapted to take the larger tubes. This made it possible to make readings over the entire period without discarding them.

THE INADEQUACY OF THE CRITERION, EQUAL INCREMENTS OF GROWTH FOR EQUAL INCREMENTS OF VITAMIN

Culture No. 7 was planted in a series of media containing different concentrations of pantothenate, and the data produced a family of parallel curves (fig. 3 in following paper). If the experiment were terminated at an arbitrary time (standard practice in nearly all assay experiments), curves could be obtained in which equal increments of vitamin appear to produce equal increments of growth. The curves in fig. 2 were obtained by readings taken at various times. At 50 hours there appears to be a straight-line relation between the amount of added vitamin and

TABLE III

THE AMOUNT OF GROWTH AFTER 72 HOURS OF CULTURES FROM PEDIGREE 1 ON BURKHOLDER'S MEDIUM DEFICIENT IN THE INDICATED VITAMINS

Culture No.	Photometer Reading			Culture No.	Photometer Reading		
	—*Py.*	—*Pa.*	—*Bi.*		—*Py.*	—*Pa.*	—*Bi.*
1 (diploid)	350	220	11	*4*	350	15	12
2 (diploid)	24	280	280	*5*	310	20	8
				7	22	200	125
			4 x 7				
10 (diploid)	315	240	135				
20	274	45	50	*12*	355	293	170
21	312	202	55	*13*	80	65	160
22	290	200	59	*14*	350	220	75
23	300	210	110	*15*	25	15	7
90	318	212	140				
91	100	210	140				
92	300	235	134				
93	345	235	110				
			4 x 20				
25				*33*	340	12	10
26	310	25	145	*34*			
27	325	28	145	*35*	410	140	100
28				*36*	355	9	9
			5 x 23				
57	305	16	33	*69*	340	237	275
58	37	94	14	*70*	93	15	
59	38	100	10	*71*	358	16	230
60	347	16	20	*72*			
86	400	315	15	*154*	355	200	120
87	380	150	150	*155*	12	165	30
88	400	300	10	*156*	425	140	300
89	460	50	200	*157*	3	20	365
			20 x 23				
136	318	256	160				
137	360	222	193				
138	340	240	200				
139	320		170				

the amount of growth over a considerable portion of the curve. However, this culture was observed continuously, and eventually nearly as much growth was attained in the medium without the added vitamin as in the one containing relatively large amounts of added pantothenate (fig. 3 in following paper).

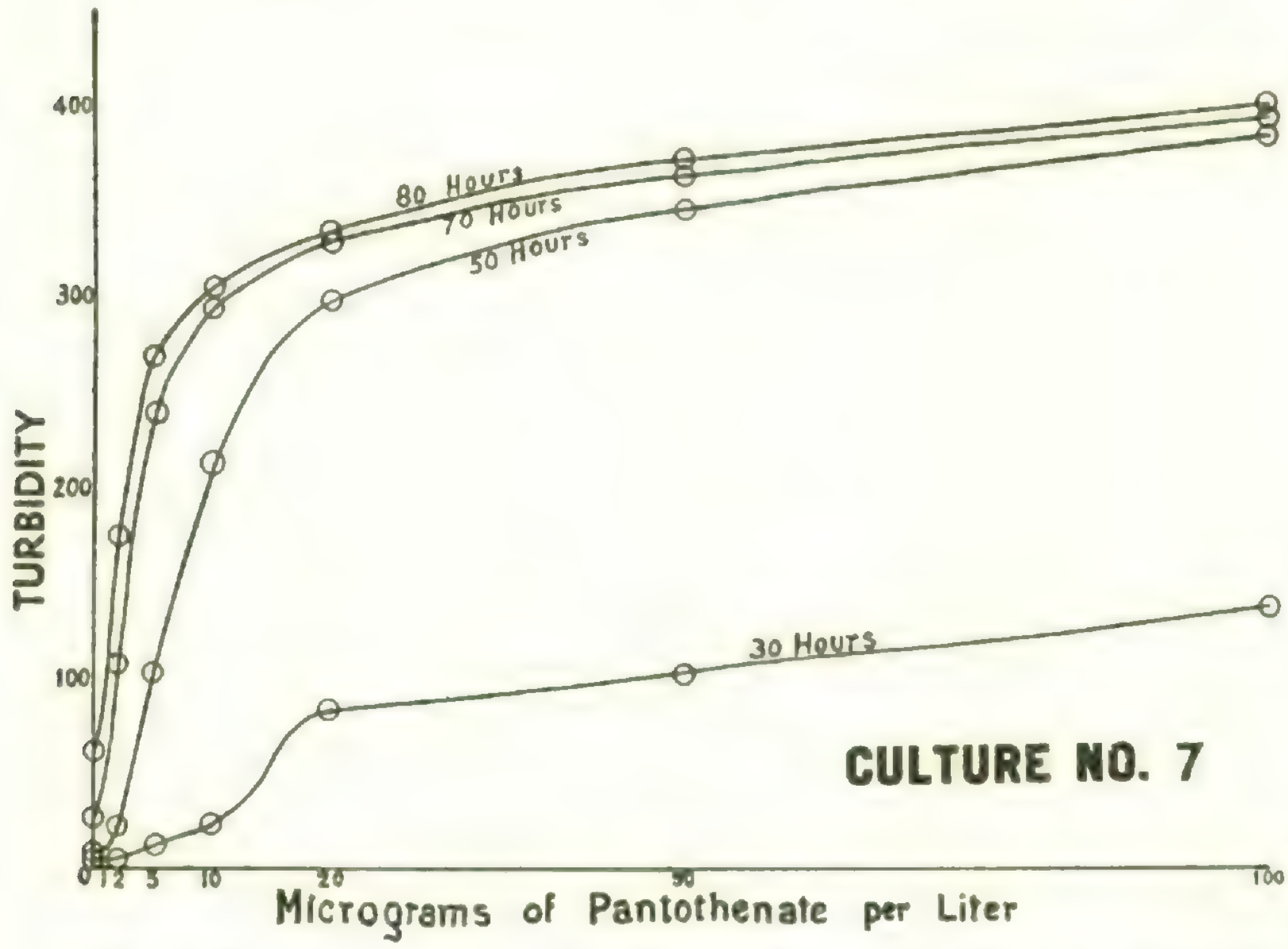

Fig. 2. The relationship between increments of pantothenate in Burkholder's medium and the amount of growth of culture No. 7 at different time intervals. In some phases of the curves a straight-line relationship exists between the amount of growth and the amount of added pantothenate but in all the culture tubes the growth eventually rose to approximately the same level.

THE EFFECT OF MULTIPLE DEFICIENCIES OF THE B VITAMINS

A haploid culture of *Saccharomyces cerevisiae* which grew well on an agar containing Hutner's synthetic medium with the vitamins, biotin, inositol, thiamin, and pantothenate, but which was unable to grow on the same agar medium lacking all these vitamins, was tested on agar containing various combinations of vitamins. Pour plates following Lederberg and Tatum's ('46) technique were made. In this technique a layer of sterile agar is poured in the bottom of the petri dish, then a layer of agar seeded with 500 cells poured on top, and a third layer of sterile agar on top of the second. This technique prevents colonies at the top and bottom of the agar from growing diffusely over or under the agar. A penicillin assay cup placed in the center of each plate was filled with a solution containing the combinations of vitamins.

Colonies were counted and a number of methods of scoring were tested, but simple + and — scoring is probably the most informative. The following tabulation gives the results:

VITAMINS PRESENT	VITAMINS ABSENT	SCORE
B I Th Pa		+ + + +
I Th Pa	B	+ + +
B Th Pa	I	+ + + + +
B I Pa	Th	+ +
B I Th	Pa	+ + +
Th Pa	B I	+ +
I Pa	B Th	+ +
I Th	B Pa	+ + +
B Pa	I Th	+
B Th	I Pa	−
B I	Th Pa	+
Pa	B I Th	+
Th	B I Pa	+
I	B Th Pa	+ +
B	I Th Pa	−
	B I Th Pa	−

The addition of inositol is apparently not very helpful in this concentration (10,000 γ per liter) when biotin, thiamin, and pantothenate were also present, for there was more growth when it was absent than when it was present. Actually there were fewer colonies when it was absent, but those which grew did much better. However, the culture supplied pantothenate alone grew less well than that supplied both inositol and pantothenate. There were probably considerable amounts of biotin in the agar, for removal of biotin did not usually reduce growth greatly. Removal of biotin and inositol simultaneously was serious. When either inositol or pantothenate were removed singly no serious effect occurred, but when both were removed together there was considerably less growth. The cells could synthesize both inositol and pantothenate easily when only one was absent but lacking both they synthesized poorly. These facts indicate that inability to grow in the absence of vitamins may involve simply lack of capacity to grow, or begin to grow, under the prescribed conditions rather than inability to synthesize the absent vitamins under all conditions (Williams, '41).

THE RELATION BETWEEN VIABILITY OF CELLS AND INABILITY TO GROW ON DEFICIENT MEDIUM

The ability or inability to grow in a deficient medium may merely involve inviability in the new medium rather than absolute inability to synthesize the vitamin in question. If the cells are inviable in the deficient medium they will be unable to begin synthesis of the required vitamin. The fact that most yeasts begin to synthesize when they are permitted to stand a sufficiently long time suggests that continued examination of cultures is necessary. This points up an important difference between *Neurospora* and yeasts. A conidium of *Neurospora* can put out a germ-tube and begin growth in distilled water, but if it is to continue growth

it must be immediately supplied with the substances which it requires. It is relatively difficult to establish a *dormant mycelium* capable of awaiting future developments. Probably one of the most important advantages of a single-celled form over a filamentous fungus is that the single-celled form can go through one or two divisions and settle down to dormancy while a filamentous organism with specialized spores must continue to grow once the filament is produced or it will perish. This may give the appearance of absolute deficiencies to many mutants which die shortly after producing a filament in a medium lacking a specific vitamin.

These results have been supported by further work on three other mutants differentiated by ability to synthesize paraminobenzoic acid, pyridoxine, and uracil. So-called nonsynthesizers of pyridoxine eventually grew in a medium containing no added pyridoxine. Diploids heterozygous for a gene controlling synthesis of paraminobenzoic acid produced two classes of offspring, one which grew rapidly and one which grew slowly in the absence of paraminobenzoic acid. Although these two classes were clearly differentiated, the weak synthesizers were always able to grow eventually. An even more important bit of confirmatory evidence was obtained from the stock incapable of synthesizing uracil. The uracil-deficient cultures responded quickly to large amounts of uracil added to Burkholder's medium, but in the medium without added uracil they died. Transfer from uracil-deficient medium to a complete medium a few days after inoculation proved that the cells had died.

CONCLUSIONS

(1) Our results indicate that all so-called "nonsynthesizing" yeasts which remain alive when incubated in a deficient medium will eventually grow and synthesize vitamins in that medium.

(2) We have decided that Burkholder's conclusion that certain yeasts are "nonsynthesizers" requires qualification because synthesis might have been discovered if observation were made over a longer period.

(3) We suggest that many of Beadle and Tatum's "vitaminless" mutants may appear to be "nonsynthesizers" because they die in the deficient medium. "Reversions" of *Neurospora* mutants to wild-type, i. e., slow growth of "vitaminless" mutants in the deficient medium have been reported by Bonner, Tatum, and Beadle ('43) and other workers in this field, but they are usually regarded as exceptional cases rather than the standard expected behavior. The above results suggest the possibility that an improvement of the medium, without addition of the vitamin for which the stock is deficient, might lead to a higher frequency of reversions.

A DIRECT RELATIONSHIP BETWEEN PANTOTHENATE CONCENTRATION AND THE TIME REQUIRED TO INDUCE THE PRODUCTION OF PANTOTHENATE-SYNTHESIZING "MUTANTS" IN YEAST[1]

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This paper describes experiments indicating that the concentration of pantothenate bears a direct relation to the time required to restore pantothenate synthesis in a yeast cell. Various members of the pedigree shown in Table II[2] were grown in batches of Burkholder's medium made up with the following amounts of pantothenate added per liter: 100, 50, 20, 10, 5, 2, 1, 0.5, and 0 γ. Each tube was inoculated in a uniform manner with a loop. Three hundred colonies grew from each loopful of cells on plating, but since the haploid cells were typically aggregated the total number of cells was probably less than 1500.

Figure 3 shows the results with S. *cerevisiae* (culture No. 1), the turbidity being plotted against time in hours. The graphs are made by plotting the average of the turbidity produced in duplicate tubes, except in a few cases in which the tubes were so widely different that averaging did not seem to be a permissible practice. Usually the readings differed by only a few units and averaging was obviously acceptable. After 45 hours, growth is practically completed in the media containing 50 and 100 γ of pantothenate, but it is fully 75 hours before appreciable growth is recorded in the tube without the added pantothenate. This culture had previously been characterized as a synthesizer of pantothenate. These data show that diagnosis depends largely on the time at which readings are taken. Comparison of the 100 γ and 0 γ tubes at the end of 45 hours would have resulted in characterizing this particular organism as a "nonsynthesizer" of pantothenate. The relationship between the amount of added pantothenate and the time at which growth begins is quite clear, since the curves are all closely parallel during early and logarithmic growth and overlapping occurs only after the logarithmic phase of growth has been completed. There is a sharp difference between the time at which growth begins in the tubes containing 0.5 and 1 γ of pantothenate per liter as well as between growth in tubes containing 1 and 2 γ of pantothenate per liter.

The culture of S. *cerevisiae*, whose reactions are recorded in fig. 3, was induced to sporulate, and similar tests with the four haplophase cultures are shown in figs. 4 and 5. Cultures No. 3 and No. 4 are remarkably similar in behavior. According to previous techniques, these would have been classified as "nonsynthesizers" because growth in the absence of pantothenate did not begin until after 250 hours. The particularly interesting feature of the behavior of these cultures is the direct relation between the length of the delay before growth begins and concentration of pantothenate in the medium.

[1]This work was supported by grants from Anheuser-Busch, Inc., The American Cancer Society, and Washington University.
[2]See preceding paper.

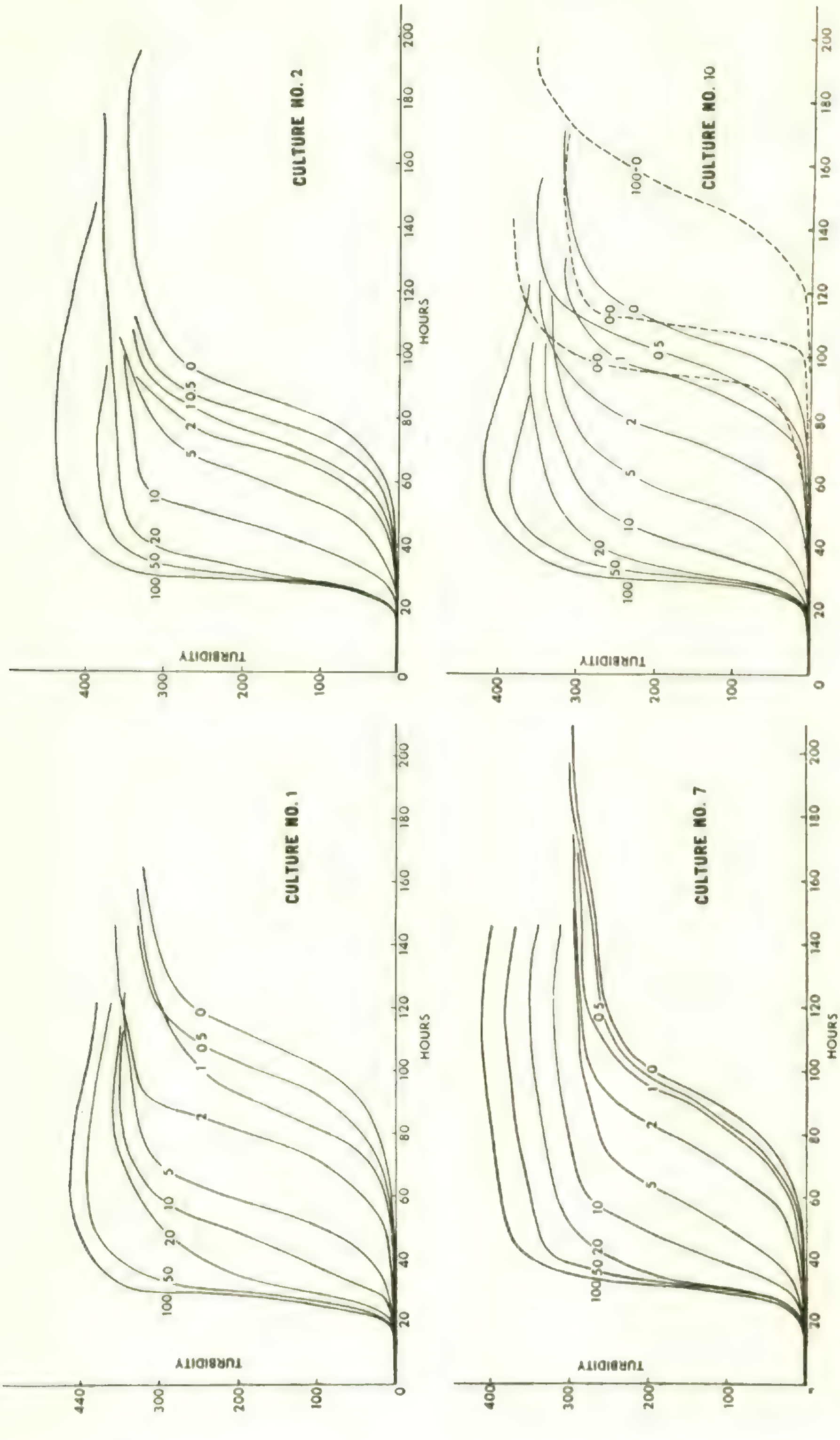

Fig. 3. The growth of cultures Nos. 1, 2, 7, and 10 in Burkholder's medium containing different concentrations of pantothenate. The solid lines represent the original inoculations; the dotted lines represent transfers from the 100 to 0.

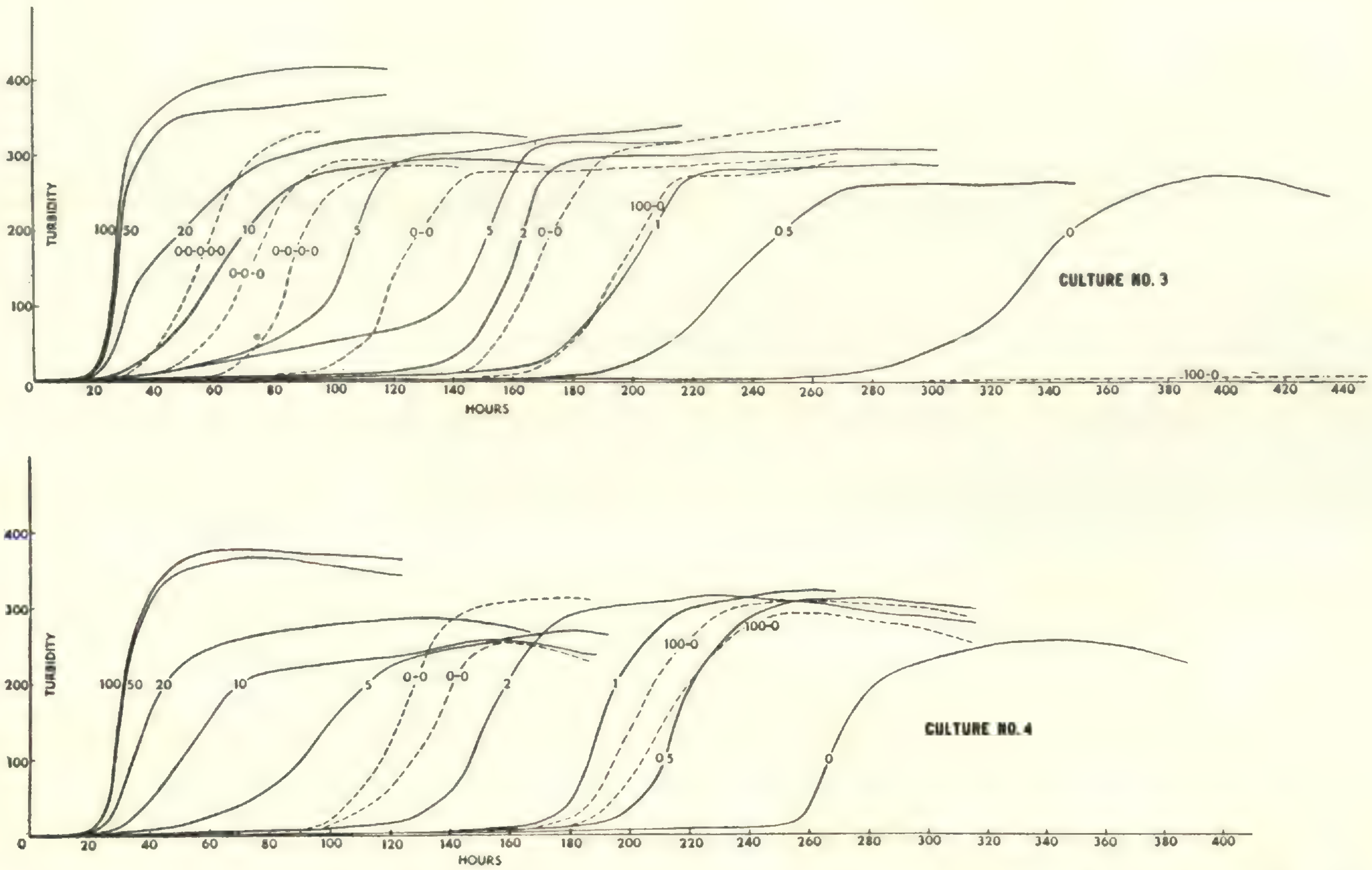

Fig. 4. Growth of cultures Nos. 3 and 4 on Burkholder's medium containing different concentrations of pantothenate. (The solid lines represent the original inoculations; the dotted lines represent transfers from these inoculations as indicated, 100–0 being a transfer from 100 to 0).

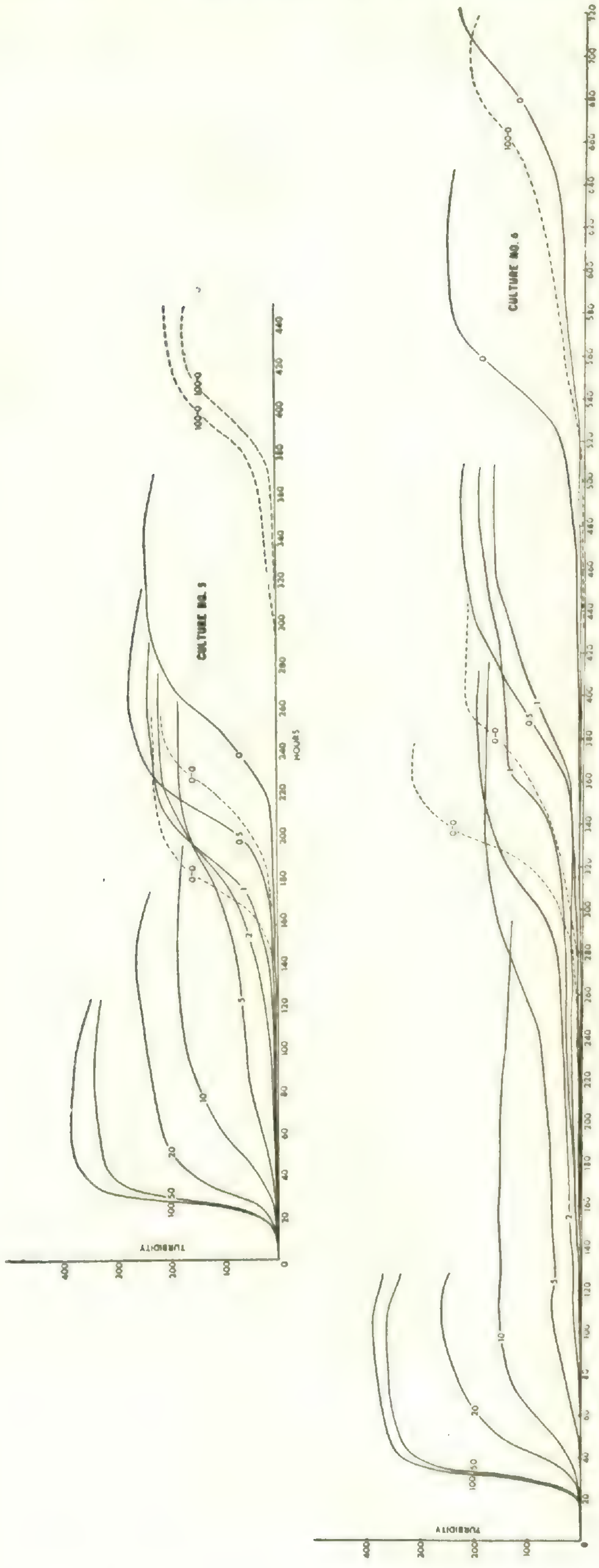

Fig. 5. Growth of cultures Nos. 5 and 6 on Burkholder's medium containing different concentrations of pantothenate.

In culture No. 5 (fig. 5) the different concentrations of pantothenate also bear a direct relation to the delay before growth begins. A similar picture exists for culture No. 6 (fig. 5), except that in the concentration of 1 γ and 0 γ per liter the duplicate tubes differed so markedly from each other that it was not permissible to average the results. This is one of the few cases in which growth in 1γ per liter in one of the duplicate tubes occurred later than that in the tube containing 0.5 γ per liter.

The behavior in culture No. 5 (fig. 5) shows an almost ideal example of general tendency of the "delayed" cultures. Growth in media containing 100 and 50 γ per liter takes place at a very rapid rate. In the medium containing 20 γ the rate is somewhat decreased, and in 10 γ considerably so. A further decrease occurs in 5 γ per liter, so that there is a continual decrease in rate of growth in the 50, 20, 10 and 5 γ media, respectively. The case is quite different in the 2, 1, 0.5 and 0 γ media, where beginning of growth is delayed more and more as the concentration decreases but once growth begins the rate is uniform and more rapid than in the 5 γ medium. The decreasing rate in the first five curves indicates that where there is an excess of pantothenate the growth bears a direct relation to the concentration of pantothenate, indicating that synthesis is suppressed when more than 5 γ per liter are present. (See also culture No. 4, fig. 4).

The rate of growth in the last four curves is practically identical, but the delay before growth begins bears a direct relation to the concentration of pantothenate. This is interpreted to mean that in each of the last four curves the growth begins after the induction of a "mutation" which possesses the ability to synthesize pantothenate and that the rate of growth depends on the synthesis of the vitamin by the cell. The basic assumption for this interpretation is the view that *de novo* mutations from inability to ability to synthesize are extremely infrequent and the mutations observed in the laboratory are practically all "loss" mutations. On this assumption, an agent which produces regular and precise changes in cells from "nonsynthesizers" to "synthesizers" does not produce a change of a completely non-existent locus to a synthesizing locus but merely acts to bring a partially degraded or temporarily inactive gene into functional activity. The rate of growth is independent of the concentration of pantothenate originally present in the medium (below 2 γ per liter). However, the time at which the "mutation" is induced (the "delay") depends on the concentration of pantothenate present; possibly directly on the number of molecules of pantothenate impinging on the gene. In a medium containing 1 γ per liter, more molecules would collide with any given surface than in one containing 0.5 γ per liter. The fact that only a small number of cells was used in inoculating the tubes and that easily detectable and constant differences exist between the low concentrations indicate that mutation occurs in many of the viable cells in a given tube at approximately the same time, rather than that one cell mutates and then outgrows its neighbors. If the latter were the case, the curves would overlap and the precise differences between the different concentrations would not be detectable. It

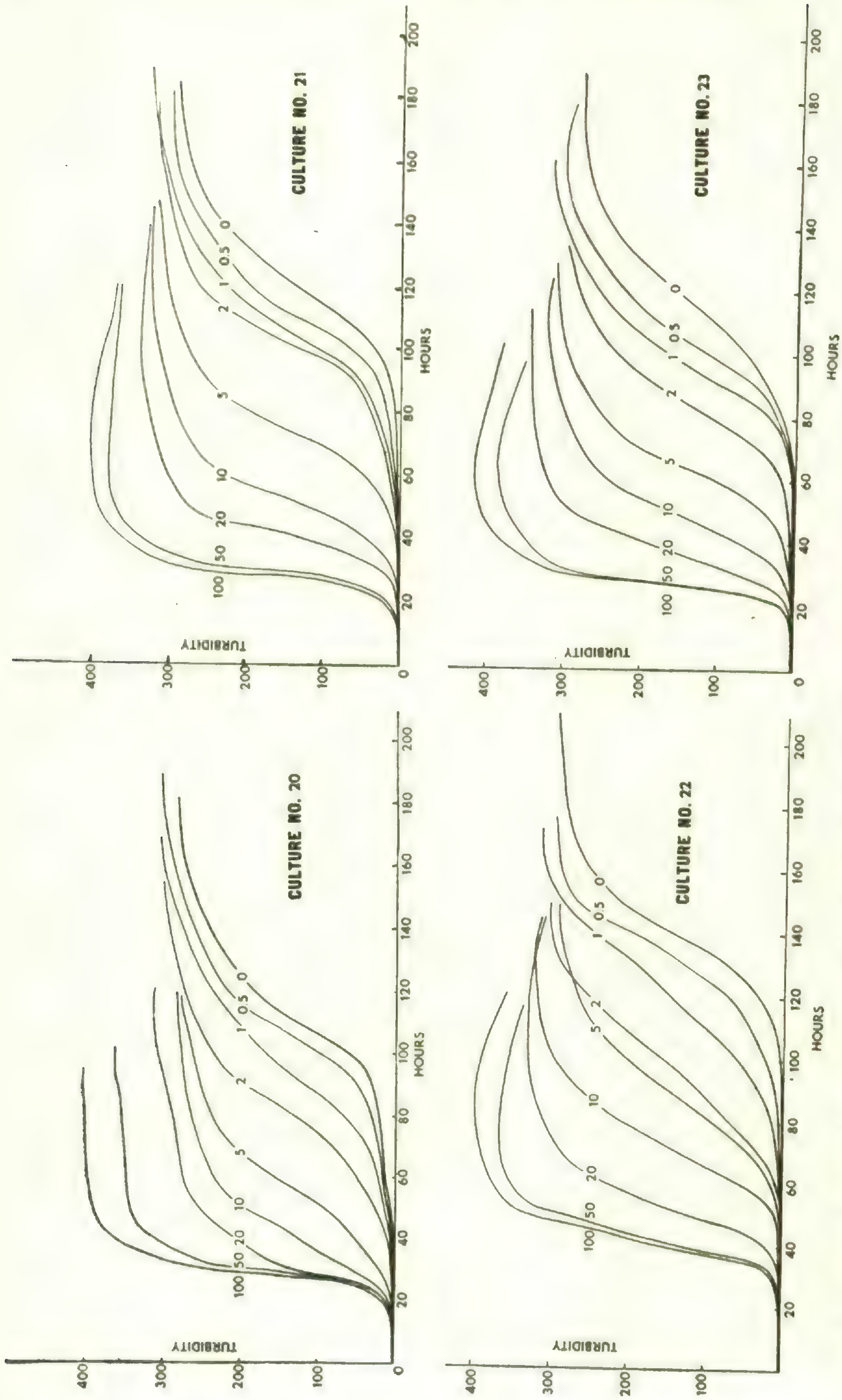

Fig. 6. Growth of cultures Nos. 20, 21, 22, and 23 on Burkholder's medium containing different concentrations of pantothenate.

is, of course, difficult to call these organisms "mutants" because the specific test for mutation is segregation. When transfers from the culture tubes without the added pantothenate were made to similar tubes likewise without added pantothenate (0–0) growth occurred about 150 hours sooner in the second than in the original test. These curves of growth are shown as dotted lines on the graph. As the yeast was transferred serially in the 0 medium, the delay before growth started was further shortened. The fifth transfer (0–0–0–0–0) began to grow sooner in the medium without the addition of pantothenate than the cultures which had been originally classified as synthesizers.

The original cultures came from a slant of yeast extract agar. Cells were suspended in 10 cc. sterile distilled water, and transfers to Burkholder's medium were made with a loop of this diluted suspension to insure against transfer of vitamins. A small but uniform number of cells was transferred in each loop. Irrespective of the concentration of pantothenate in Burkholder's synthetic media none of these original transfers failed to grow, but each grew after the delay indicated on the graphs. Many other transfers were subsequently made from one tube of Burkholder's synthetic medium to another with the same concentration of pantothenate; all these resulted in growth. Generally speaking, 0–0 transfers began growth much sooner than the original transfer, indicating that a "mutation" had occurred in the first transfer and that growth began due to the "mutation" or that some new channel of synthesis was established which became more efficient with continued use.

Saccharomyces carlsbergensis (culture No. 2, fig. 3) is an undelayed synthesizer of pantothenate, and growth in all concentrations of pantothenate is completed before 100 hours. The single haploid offspring of *S. carlsbergensis* (No. 7, fig. 3) is smiliarly an undelayed synthesizer but is spectacularly capable of utilizing any available pantothenate, as is shown by the beautifully parallel curves on the different concentrations. A hybrid between undelayed synthesizer (culture No. 7) and delayed synthesizer (No. 5) produced the hybrid culture No. 10, which was an undelayed synthesizer (fig. 3). When four haploid progeny from hybrid No. 10, cultures Nos. 20, 21, 22, and 23 (fig. 6), were tested, all showed the ability to use whatever pantothenate was available, as evidenced by the parallel nature of the curves for different concentrations. However, these four progeny were all undelayed synthesizers of the vitamin, and no clear-cut Mendelian segregation occurred. This does not necessarily mean that the difference is not one under gene control, for this pedigree is one in which gene transformation frequently occurs. This matter is being dealt with in an article now in press (Lindegren and Lindegren, '47). The pantothenate character segregates regularly in other pedigrees in which Mendelian segregation of other gene-determined characters normally occurs.

DISCUSSION

Non-Random "Mutation."—Mutations are generally supposed to result from random changes in the gene which occur independently of substrate with a specific

frequency. The probability that spontaneous or induced mutations would produce adaptive or "progressive" changes in a gene are generally thought to be about as likely as that the act of throwing a wrench at a motor would result in an improvement in the machine. Skoog and Lindegren ('47) have presented evidence indicating that mutation to glucose utilization was influenced by the nature of the substrate. The above data suggest that "mutation" which enables the cell to synthesize pantothenate depends directly on the concentration of pantothenate in the environment. The "mutations" induced by pantothenate are quite different from the ordinary recessive mutations used in genetical Mendelian analysis; they may merely be the result of the addition to the gene of one of its essential components. Such a component might correspond to what I have called the *cytogene*.

This presupposes that pantothenate synthesis is under genetic control. Most previously described "vitaminless" mutants are probably genotypes unable to survive in the deficient synthetic medium. The genotypes which we described here synthesize pantothenate when the level of pantothenate in the medium drops below a certain minimum. However, it is suggested by the data that some pantothenate (either in the cell or in the medium) must be present before the synthesizing mechanism can operate.

Organized versus Molecular Genes.—The gene is probably a loosely organized complex structure rather than a precisely definable chemical compound. The tendency to conclude from (1) the experiments of Stanley (in which an isolated crystalline nucleoprotein was shown to produce the same effect as tobacco mosaic virus) and from (2) the experiments of Avery, McLeod, and McCarty (in which a nucleic acid was shown to be capable of transforming one type of pneumococcus into another) that the gene is either a crystalline nucleoprotein or a nucleic acid disregards the possibility that the nucleoprotein and the nucleic acid may be only a part of the organized structure making up the gene. The fact that thousands of molecules of the mosaic virus nucleoprotein are required to produce a single infection has been interpreted to result from the difficulty of securing infection with a single particle. An alternative interpretation is possible: it may be that only one particle in a thousand of the "purified" preparation is so organized that it is capable of infection. In the pneumococcus experiment the transformation may have been achieved because the complex which comprised the gene producing the smooth mutant form was brought into functional activity by the addition of a single nucleic acid, just as a machine can be made to operate by adding a single nut. This does not mean that the nucleic acid is the gene, any more than the nut is the machine. Our experiments with pantothenate show that by adding molecules of it to a suspension of yeast cells a cell incapable of synthesizing pantothenate could be transformed into one capable of performing the synthesis. The fact that a gene-controlling synthesis has become functional may not mean that a gene has been added but merely that one component of the complex which makes up the gene has been supplied. This component, though essential, may be only a part of the total organized structure.

CONCLUSIONS

The evidence presented above indicates that in the presence of a large excess of pantothenate no synthesis of pantothenate occurs although growth of cells by utilization of the available pantothenate goes on at a very rapid rate. At concentrations not in excess of, but greater than the minimum required for growth, the cells do not synthesize, and the rate at which they grow is determined by the amount of pantothenate supplied. When the concentration of pantothenate is less than the minimum required for growth the cells "mutate" so that they are able to synthesize pantothenate and grow. The time required for this "mutation" to take place is determined by the small amounts of pantothenate which are present in the media. The data may not completely exclude the possibility that only a small fraction of the population has been affected and that selection has been an important factor in the phenomenon; further tests of this view are in progress. The present indications support the view that a large fraction of the population is involved and if this be true, pantothenate can be regarded as an agent which acts to repair a partially degraded gene. The data suggest that in the complete absence of pantothenate neither synthesis nor growth can begin. (The cells in the medium to which no pantothenate has been added did not necessarily begin growth in the absence of pantothenate, for each cell probably carried a sufficient amount to initiate growth.) Synthesis occurs in Burkholder's medium only if enough pantothenate to initiate synthesis but not enough to suppress it is present.

ACKNOWLEDGMENTS

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MENDELIAN INHERITANCE OF GENES AFFECTING VITAMIN-SYNTHESIZING ABILITY IN SACCHAROMYCES[1]

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Pedigrees describing both Mendelian and non-Mendelian inheritance of the ability to ferment carbohydrates in *Saccharomyces* have been reported by us (Lindegren and Lindegren, '47). Genes controlling the fermentation of galactose, maltose, or melibiose are transmitted in a regular Mendelian manner in some pedigrees, and in a non-Mendelian manner in others. Present indications are that this is due to the gene-to-gene transfer of some essential gene-component controlling fermentation. This phenomenon complicated the problem of genetical analysis of yeasts until regular Mendelian pedigrees were available.

The diagnosis of the fermentative ability of any selected culture is clear-cut, no difficulty being experienced in distinguishing a fermenter from a non-fermenter. In the present pedigree the fermentation of sugar is usually complete after 48 hours; the negatives do not ferment when held for three weeks. When regularly segregating pedigrees became available, the problem of genetical analysis of fermentative ability was capable of an uncomplicated solution.

Burkholder's medium (Lindegren and Raut, '47) is an excellent diagnostic medium for distinguishing pantothenate "synthesizers" from "nonsynthesizers," because a so-called nonsynthesizer grows rapidly in this meduim containing pantothenate, but requires weeks or months to produce growth in its absence. However, genes affecting vitamin synthesis are apparently transmitted in some pedigrees in a non-Mendelian way similar to that displayed by genes controlling fermentation. The first pedigree on the inheritance of "vitamin-synthesizing" ability in *Saccharomyces* (Lindegren, '45) failed not only to reveal regular Mendelian inheritance of this ability but also of genes controlling the fermentation of carbohydrates. In our selected inbred strains, the ability to ferment galactose and maltose is transmitted in a regular Mendelian manner, and the present paper shows that genes affecting the synthesis of paraminobenzoic acid, pantothenate, pyridoxine, and thiamin are transmitted with corresponding regularity. These genes are described as "affecting" rather than "controlling" the synthesis of vitamins, because we have not discovered any absolute deficiencies in yeasts. Lindegren and Raut have shown that a so-called nonsynthesizer of pantothenate eventually will grow in a medium without the addition of pantothenate, although some cultures do not begin growth until they have stood in the tubes for nearly a month.

[1]This work was supported by grants from Anheuser-Busch, Inc., Washington University, and the American Cancer Society.

In genetical analysis, it is relatively unimportant whether absolute or partial deficiencies are dealt with; all that is required is a clear-cut differentiation of the haploid offspring of a hybrid into two different categories. This is easily effected in our present yeast pedigrees by using Burkholder's medium with and without added pantothenate. Genes affecting pantothenate and pyridoxine synthesis are easily diagnosed; the "nonsynthesizers" do not begin to grow until a week after planting while the "synthesizers" attain nearly full growth after 48 hours. The former may produce a turbidity reading of between 200 and 300, while the latter still show a reading of between 0 and 5. After the tubes have been held for two months it is difficult to distinguish them, but at 4 or 5 days the difference is pronounced. Cultures differing in genes which affect the synthesis of thiamin and paraminobenzoic acid show distinct differences at the end of 48 hours, but by the fourth day it is difficult to tell them apart. However, any clear-cut segregation of the progeny into two classes supplies the geneticist with an adequate gene "marker."

Table I describes 8 asci dissected from a hybrid heterozygous for mating type,

TABLE I

ANALYSIS OF ASCI FROM A HYBRID HETEROZYGOUS FOR MATING TYPE, FERMENTATION OF GALACTOSE AND MALTOSE, AND GENES AFFECTING THE SYNTHESIS OF PANTOTHENATE

(Ascospores from Hybrid 1426 × 1428 (α G ma pan × a g MA PAN))

Culture No.	Type	G	MA	PAN	Culture No.	Type	G	MA	PAN
	1					2			
2101	a	−	−	274	2105	a	+	−	5
2102	a	−	−	160	2106	a	−	+	190
2103	α	+	+	3	2107	α	−	+	2
2104	α	+	+	4	2108	α	+	−	254
	3					4			
2109	a	−	+	6	2113	α	−	−	3
2110	α	+	−	2	2114	α	−	+	210
2111	α	−	−	145+	2115	a	+	−	220
2112	a	+	+	274	2116	a	+	+	0
	5					6			
2121	a	−	+	0	2125	a			2
2122	α	+	−	200	2126	α	+	+	270
2123	α	+	−	5	2127	a	−	−	4
2124	a	−	+	345	2128	α	−	−	200
	7					8			
2147	α	+	+	290	2151	α		+	4
2148	a	−	+	137+	2152	α		+	250
2149	a		−	3	2153	a		−	140+
2150	α		−	8	2154	a		−	4

galactose fermentation, maltose fermentation, and a pair of genes affecting the ability of the organism to grow in Burkholder's medium without added pantothenate. The — and + signs under the columns G and MA indicate whether or not the organism produced gas in a medium containing galactose or maltose respectively. The figures under the column PAN show the turbidity reading registered in a Klett Photoelectric Colorimeter, after four days in a culture tube of Burkholder's medium without added pantothenate.

TABLE II

ANALYSIS OF ASCI FROM A HYBRID HETEROZYGOUS FOR MATING TYPE, FERMENTATION OF GALACTOSE AND MALTOSE, AND GENES AFFECTING THE SYNTHESIS OF PARAMINOBENZOIC ACID, THIAMIN AND PYRIDOXINE.

(Ascospores from Hybrid 2236 × 2090 (a G MA pab th py × α g ma PAB TH PY))

Culture No.	Type	G	MA	PAB	TH	PY	Culture No.	Type	G	MA	PAB	TH	PY
1							4						
2409	α	+	−	−	−	+	2419	α	−	−	+	+	−
2410	a	−	−	+	+	−	2420	a	−	+	+	−	−
2411	α	+	+	−	−	+	2421	a	+	+	−	+	+
2412	a	−	+	+	+	−	2422	α	+	−	−	−	+
5							6						
2423	α	−	−	−	−	−	2427	a	+	−	+	+	−
2424	α	+	+	+	+	+	2428	α	−	+	−	−	+
2425	a	+	−	−	−	+	2429	α	−	−	−	+	−
2426	a	+	+	+	+	−	2430	a	+	+	+	−	+
7							8						
2431	a	+	+	−	+	−	2435	a	+	−	−	−	+
2432	a	+	−	+	+	+	2436	a	−	+	+	+	−
2433	α	−	+	+	−	+	2437	α	−	−	+	−	+
2434	α	−	−	−	−	−	2438	α	+	+	−	+	−
9							10						
2439	α	+	−	−	−	−	2443	a	+	+	+	−	−
2440	α	−	+	+	+	+	2444	a	−	+	−	−	+
2441	a	−	+	−	+	+	2445	α	+	−	+	+	−
2442	died						2446	died					
11							12						
2447	a	−	−	+	−	−	2451	a	−	−	+	−	+
2448	α	+	−	−	+	+	2452	α	+	+	+	+	+
2449	a	−	+	+	+	−	2453	α	+	+	−	+	−
2450	α	+	+	−	−	+	2454	a	−	−	−	−	−

TABLE II (Continued)

Culture No.	Type	G	MA	PAB	TH	PY
13						
2455	α	+	−	−	−	+
2456	a	−	+	+	−	+
2457	α	−	+	+	+	−
2458	a	+	−	−	+	−
14						
2459	α	+	+	−	−	−
2460	a	+	−	−	−	+
2461	α	−	−	+	+	+
2462	a	−	+	+	+	−
15						
2463	a	+	+	−	−	+
2464	α	−	+	+	+	−
2465	a	−	−	+	+	−
2466	α	+	−	−	−	+
16						
2467	a	+	−	−	−	−
2468	α	−	−	+	+	+
2469	a	+	+	−	−	+
2470	α	−	+	+	+	−
17						
2471	α	+	−	−	+	−
2472	a	−	+	+	+	−
2473	α	+	−	+	−	+
18						
2474	α	−	+	−	−	−
2475	a	+	−	+	+	+
2476	a	+	+	−	−	+
19						
2477	a	+	+	+	+	−
2478	α	−	−	−	+	−
2479	a	+	+	+	−	+
2480	α	−	−	−	−	+
20						
2481	a	+	−	−	+	−
2482	α	−	−	+	−	+
2483	α	−	+	−	+	−
2484	a	+	+	+	−	+
21						
2485	α	+	+	−	+	+
2486	a	−	+	+	−	+
2487	a	+	−	+	+	−
2488	α	−	−	−	−	−
22						
2489	α	+	+	+	+	−
2490	a	−	−	−	+	+
2491	α	+	+	−	−	−
2492	a	+	−	+	−	+
23						
2493	α	+	−	−	+	−
2494	α	−	−	−	−	+
2495	a	+	+	+	+	−
2496	a	−	+	+	−	+
24						
2497	α	+	+	−	+	−
2498	α	−	−	+	+	+
2499	a	−	−	−	−	−
2500	a	+	+	+	−	+
25						
2501	a	−	−	+	−	+
2502	a	−	−	+	+	−
2503	α	+	+	−	+	−
2504	α	+	+	−	−	+
26						
2505	a	+	−	+	−	+
2506	α	−	−	−	+	−
2507	α	+	+	+	−	+
2508	a	−	+	−	+	−

Cultures 2111, 2148, and 2153 produced the recorded turbidity in the pantothenate-free medium after 48 hours and were discarded. They would doubtless have grown more, this being indicated by the + sign after the turbidity reading. Each ascus produced two cultures with a turbidity reading of less than 8 and two with more than 160 four days after inoculation. The genes controlling mating type, galactose fermentation, and maltose fermentation also segregated regularly in each of the eight asci.

Table II is a pedigree describing the cultures grown from the ascospores dissected from 24 asci. These asci are derived from a hybrid heterozygous for mating type, galactose fermentation, maltose fermentation, and genes affecting the synthesis of paraminobenzoic acid, thiamin, and pyridoxine. The + and — signs indicate whether or not the cultures ferment galactose or maltose, and whether they grow in Burkholder's vitamin-free medium. The readings on the paraminobenzoic- and thiamin-free media were made after 48 hours, while those in the pyridoxine-free medium were made after four days. Two of the cultures from each ascus produced heavy turbidity in the vitamin-free media while two produced practically no growth at the time diagnosis was made. The readings were all recorded numerically just as were the pantothenate readings shown in Table I, but for the purposes of clarity were converted into + and — signs in the table. The only exception to the expected Mendelian segregation of 2:2 in each ascus is found in asci Nos. 5 and 22 in which three fermenters of galactose were discovered, although the mating type, maltose fermentation, and vitamin characters segregated regularly.

Tests were made for linkage between all possible pairs of genes, and usually free assortment was indicated. In some cases linkage to each other or to different centromeres was suggested but the evidence was not sufficient to warrant definite conclusions. These data are presented to establish the fact that genes affecting vitamin synthesis may segregate in a regular Mendelian manner in selected inbred pedigrees.

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AMERICAN ORIGIN OF THE CULTIVATED CUCURBITS[1]

I. Evidence from the Herbals
II. Survey of Old and Recent Botanical Evidence

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INTRODUCTION

There are four species of *Cucurbita* that rank as cultivated plants (*C. Pepo* L.; *C. moschata* Poir.; *C. maxima* Duch.; and *C. ficifolia*[2] Bouché), and there is good archeological evidence that the first three were present in the Americas in pre-Columbian times (see Carter, '45). However, it has never been decisively demonstrated that this group may not have been common to both Old and New Worlds as seems to have been the case with the white-flowered gourd, *Lagenaria sicereia* (Molina) Standl.

In the course of his investigation on the association of the cultivated cucurbits with the various Amerind cultures of the Southwest, the writer had occasion to examine most of the published work that concerns the origin of this group. The present report is an attempt to evaluate this evidence, and draw the indicated conclusions.

With the exception of *Cucurbita ficifolia*, the four species with which we are concerned are annuals. All have 20 pairs of chromosomes. They rarely, if ever, produce species hybrids, except by means of artificial pollination, and then only with difficulty. Up to the present, none have been discovered in the indigenous state.

I. EVIDENCE FROM THE HERBALS

The herbals of the 16th and early part of the 17th centuries are invaluable sources of information in tracing the origins of the cultivated species of *Cucurbita*. Prior to the establishment of contact with the New World in 1492, the herbals contained no recognizable description or illustration of these plants. Surely plants as large and distinctive in vine and fruit as squash and pumpkins would not have escaped the notice of an astute group of observers such as the herbalist-scholars of the 15th century appeared to be. A century after the discovery of America, the record as traced through the various herbals indicates that two of the annual

[1]An investigation carried out while a Fellow of the John Simon Guggenheim Memorial Foundation, 1946–1947. The writer is grateful to the Director, Librarian, and staff of the Missouri Botanical Garden for their courtesy in making available for study the excellent collection of pre-Linnean literature found at that institution. Thanks are due to Professor Edgar Anderson for his customary stimulating advice and criticism.

[2]*Cucurbita ficifolia* is ordinarily not thought of as a cultivated plant. The work of the Russian investigators Bukasov, Zhiteneva ('30), Parodi ('34), and more recently the collections of Sauer, West, and others (personal communications), indicate that it has a long history of cultivation, and must be regarded as a cultigen. There are no archeological records of its occurrence. It is a perrenial with 20 pairs of chromosomes.

species of *Cucurbita* had reached Europe, and one of them *(C. Pepo)* was represented by several varieties.

Fuchs (1542) seems to have been the first herbalist to note a cultivated cucurbit and produce a recognizable figure of it. His illustration, labelled "Türckisch Cucumer," is evidently some variety of *Cucurbita Pepo* (pl. 11, fig. 1). The deeply lobed leaves and general appearance of the plant suggest that it may be allied to our present-day Vegetable Marrows. From the shape of the fruit, there is reason to believe that the illustration labelled "Meer Cucumer" is a variety of *C. Pepo* currently known as "Small Sugar" (pl. 11, fig. 2). Like the illustrations of most herbalists, Fuchs' are somewhat conventionalized, in order to accommodate the plants to the size of the wood block, but there is no doubt that the figures mentioned are properly referable to *C. Pepo.*

Matthiolus (1560) has an illustration of what seems to be a field pumpkin *(C. Pepo)* labelled *Cucurbita indica* (pl. 12, fig. 1) Daléchamps (1587) has a copy of this plate, which Seringe (1828) improperly assigns to *C. moschata.* Although the leaves are not as strongly dissected as typical *C. Pepo,* the pattern of the remaining morphological characteristics makes it seem certain that the plant is referable to this species.

Dodoens (1563) has produced a figure *(Pepones lati)* of what appears to be a form of *Cucurbita Pepo.* Judging from the shape of the fruit and the lack of tendrils, this form must be closely related to the present-day variety "White Bush Scallop" (pl. 12, fig. 2). Daléchamps (1587), in his *Historia generalis plantarum,* has illustrated, for the first time, a warted variety of *C. Pepo* under the name *Cucurbita verrucosa* (pl. 12, fig. 3). Bauhin (1650-51) has a reversed copy of Daléchamps' figure, and Bailey ('29) is undoubtedly correct in assigning it to *C. Pepo* even though the leaves and flowers do not conform very closely to this species.

Lobelius (1591) illustrates five varieties of *Cucurbita Pepo (Pepo oblongus, Pepo rotundus compressus Melonis effigie, Melo-pepones latiores Clypeiformes, Melo-pepo teres,* and *Melo-pepo compressus alter).* The fruits pictured under the label *Melo-pepones latiores Clypeiformes* are identifiable without doubt as a form of the scallop-fruited summer squash, probably the variety "Golden Custard" (pl. 12, fig. 4). Although definitely *C. Pepo,* the remainder are difficult to homologize with any of our present-day varieties. In addition, Lobelius has produced the first illustration of a plant definitely referable to *C. maxima,* under the name *Pepo maximus Indicus compressus* (pl. 12, fig. 5).

Tabernaemontanus (1591) is particularly rich in the number of varieties of *Cucurbita Pepo* which are illustrated. A total of nine forms are figured, some of which can be recognized as closely allied to our present-day varieties. *Melopepo clypeatus* is undoubtedly a form of the "White Bush Scallop" summer squash; *Cucurbita capitata* is much like the former with a slightly different fruit shape. *Melo-pepo teres* and *M. compressus* are apparently bush forms since they lack tendrils. The shape of the fruit indicates that *Pepo maximus oblongus* is probably a

Vegetable Marrow type; the same is true for *Pepo Indicus minor oblongus*. The form designated as *Pepo Indicus minor rotundus* is quite similar in shape to our modern variety, "Perfect Gem." *Pepo Indicus minor clypeatus* and *Pepo Indicus minor angulosus* (pl. 12, fig. 6) are forms whose fruit shape and general appearance are strongly reminiscent of the modern "Table Queen" or "Acorn" squash.

The results of this survey provide strong evidence that none of the cultivated species of *Cucurbita* were known to the botanists of the Western World before 1492[3]. In the following century at least two species *(C. Pepo* and *C. maxima)* were recognized by the herbalists, and for one of them *(C. Pepo)* a number of varieties were known. It seems strange that *C. moschata* was not introduced into Europe during this period. There may be several reasons for this: (1) In general, this species is more subject to range restrictions by low temperatures and short days than either *C. Pepo* or *C. maxima;* (2) recent distribution data indicate that it is found only in the more inaccessible regions of Mexico, Central America, and Colombia.

Cucurbita ficifolia, with its relatively hard shell and rather coarse, stringy flesh, lacks the edible qualities of the annual species. This may have been the chief reason for its neglect by the early explorers. Furthermore, this species requires a relatively long photoperiod, and it is doubtful whether it would mature fruits in Europe, except perhaps in the extreme southern portions and under exceptionally favorable cultural conditions.

II. SURVEY OF OLD AND RECENT BOTANICAL EVIDENCE

Evidence for the Old World origin of the cultivated species of Cucurbita.—

The concept that the cultivated species of *Cucurbita* were indigenous to the Old World appears to have originated with Naudin (1856). At the beginning of his extensive and illuminating memoir, which has laid the experimental foundation for our understanding of the species of this group, he devotes a single paragraph to their origin. He states that of the six known species *(C. moschata, C. Pepo, C. maxima, C. melanosperma, C. perennis,* and *C. digitata)* the first three have been cultivated for a considerable length of time in Europe. The nativity of *C. maxima* is admittedly undetermined. It is claimed, without documentation, that *C. Pepo* has been known to the Romans and Greeks at least since the time of Pliny. According to Naudin, *C. maxima* and *C. moschata* are more modern introductions into European gardens ("leur introduction dans nos jardins ne remontant guère au dela de deux siècles").

[3]Sturtevant ('19, p. 219) has summarized this line of evidence in a remarkable lucid statement, "If we consider the stability of types and the record of variations that appear in cultivated plants, and the additional fact that, so far as determined, the originals of the cultivated types have their prototypes in nature and are not the products of culture, it seems reasonable to suppose that the record of the appearance of types will throw light upon the country of their origin. From this standpoint, we may, hence, conclude that, as the present types have all been recorded in the Old World since the fifteenth century and were not recorded before the fourteenth, there must be a connection between the time of discovery of America and the time of appearance of pumpkin and squashes in Europe."

Naudin, in discussing *Cucurbita ficifolia* (*C. melanosperma* Gaspar.), states that it was introduced into Europe about 1800 A. D., probably from southern Asia as indicated from its common name, "Courge de Siam." Reports of travelers led him to believe that at this time it was grown in China on a large scale; thus confirming his opinion that the species originated in Asia. Naudin thought that *C. ficifolia* has important potentialities as an economic plant, for use as human food if properly prepared in the immature stages, and as cattle food because of its long-keeping qualities.

In a later paper, Naudin (1859) reports further experimental work with various genera of the Cucurbitaceae. He does not make any positive statement about the origin of the cultivated cucurbits, although he infers that *C. moschata* is an Old World indigene. He states that seed of several varieties collected in India have been grown at the Museum. Since the early terminology of cucurbitaceous fruits was in much confusion, it is highly probable that Naudin has mistaken Pliny's reference to watermelons, melons, cucumbers, and gourds as including some members of the genus *Cucurbita*. There is no evidence to support the belief that Pliny was familiar with the latter group.

The widely held conviction that the three commonly cultivated species of *Cucurbita* were of other than American origin was continued by De Candolle ('83) on very slender, and for the most part, questionable evidence. Later investigators (Cogniaux, 1881; Pittier, '26; Herrera, '41) have propagated De Candolle's views without critical reexamination of their basis. From De Candolle's discussion of the origin of the four species under consideration it is apparent that he is positively in favor of an Old World origin only in the case of *Cucurbita maxima*, and there is some reason to doubt that he felt that the record was entirely convincing here. In terminating his discussion of the origin of *C. maxima* he makes the statement, "En définitive, sans ajouter une foi implicite à l'indigénat sur les bords du Niger, fondé sur le dire d'un seul voyageur, je persiste à croire l'espece originaire de l'ancien monde et introduite en Amérique par les Européens."

The best evidence De Candolle could muster for his Old World theory of the origin of *Cucurbita maxima* was Hooker's (1871) citation of localities for certain collections: i. e. "Upper Guinea. Nupe on the Niger, apparently indigenous, Barter!" Welwitsch's discovery of this species in Angola is also referred to, but there is no indication as to whether or not it was an indigenous plant. The fact that Barter's plants were collected along the banks of a large river would lead to the supposition that it was an introduced species. Welwitsch's collection was made in or around a village, and it is therefore quite likely that the plants were escapes. At best, De Candolle's arguments for an Old World origin of *C. maxima* rest on an extremely flimsy foundation.

As for *Cucurbita Pepo*, De Candolle presents the documented evidence for and against its Old World origin. His position may be summed up by stating that the historical record does not contradict the opinion that this species may be of American origin.

According to De Candolle, the origin of *Cucurbita moschata* presents an unsolved problem. However, he is inclined to attach some weight to the unproven assertion that this species was more widespread in southern Asia than in any other region during the seventeenth century. As stated previously, *C. moschata* was unknown to the botanists of the fifteenth and sixteenth centuries. The first record of its occurrence seems to be the excellent illustration published by Van Rhede in *Hortus Malibaricus* (1688). During the 17th and 18th centuries it appeared in several floras of southern Asia and Africa (Wight, 1843; Clarke, 1879; etc.). However, in no case was it claimed to be an indigenous plant.

Evidently *Cucurbita moschata* was introduced into European horticulture from southern Asia (Naudin, 1856), rather than directly from the Americas. The common names given to varieties of this species were indicative of Old World origin, i. e. "Pleine de Naples," "Pleine de Barbarie," "Muscade de Provènce," etc.

De Candolle suggests that *Cucurbita ficifolia* is of American origin, since up to the time of his investigations, all the perennial species of the genus were natives to California or Mexico, whereas the annual species were assumed to be of Old World origin. This argument has now lost whatever cogency it may have had. Bailey ('43) has described several species from North America which are undoubtedly annuals.

Evidence for the New World origin of the cultivated species of Cucurbita.—

In a critical review of certain phases of De Candolle's book, Gray and Trumbull ('83) present the evidence for an American origin of the three annual species. Their report can best be summarized by quoting directly:

> "Allusion has already been made (under *Lagenaria*) to the difficulty of distinguishing the genera of the *Cucurbitaceae*, under names by which they are mentioned by voyagers and explorers of the first century after the discovery of America; and the question of species is particularly difficult. Yet we find abundant evidence—especially as respects North America—(1) that in various parts of the country, remote from each other, the cultivation of one or more species of Cucurbits by the Indians was established before those places are known to have been visited by Europeans; (2) that these species or varieties were novel to Europeans, and were regarded by botanists of the 16th and 17th centuries, as well as by the voyagers and first colonists, as natives or denizens of the region in which they were found; and (3) that they became known only under American names; one of these names *(Squash)* becoming, in popular use, generic, and two others *(Macock* and *Cushaw)* surviving, as names of varieties, into the present century."

Gray and Trumbull then present strong evidence for their conclusions, following a chronological scheme as nearly as possible. First, the reports of several early explorers and historians are cited. Although it is usually difficult or impossible to determine precisely to what species these writers have reference, it is almost certain that they are concerned with one of the three annual species of *Cucurbita*, probably *C. Pepo*. The reports of the following explorers are cited: Columbus, Cuba, 1492; Cabeça de Vaca, Florida, 1528; De Soto, Florida and Mississippi, 1539-41; Cartier, Canada, 1535; Sagard, Canada, 1642; Lahontan, Southern Canada, 1703; also the historians who mentioned pumpkins, macocks and squashes—Captain John Smith, 1606-08; Strachey, 1610; Higginson, 1629; Beverley, 1705; and others.

Further support is provided by the works of the 16th century herbalists—Fuchs, Dodoens, Matthiolus, etc. It is clear, as Gray and Trumbull point out, that the Cucurbitas were considered foreign or novel by these botanists. Furthermore, the word "Indian" as applied to the area of origin of various species did not necessarily mean that they came from Asia, but rather the West Indies or the Americas. Much confusion has come about through a misinterpretation of the word "Indian." De Candolle and others have, for the most part, interpreted it in a narrow sense as applying only to British India, but the truth seems to be that *Cucurbita Pepo* and *C. maxima* reached Europe from the West Indies or directly from the American continent.

Gray and Trumbull regard Nuttall's (1818) statement of particular importance in establishing the American origin of the cultivated *Cucurbita*. Nuttall mentions two species, *C. Lagenaria* and *C. verrucosa* (Warted Squash), and of the latter, he observes, "Cultivated also by the Indians of the Missouri to its sources." *Cucurbita verrucosa* is one of the warted varieties of *C. Pepo*. Trumbull's work (1876) in tracing the Indian origin of the words squash, cushaw and macock is considered by Gray and Trumbull as being especially significant in establishing a case for the North American origin of *Cucurbita Pepo* and *C. moschata*. Trumbull states in summarizing his conclusions, "As regards North American varieties, the evidence seems conclusive. These varieties at least bear Indian names, which date from the first coming of the Europeans, and of these varieties we have no mention before they were found in North America."

Recent botanical evidence.—

The Russian plant explorers (Bukasov, '30; Zhiteneva, '30) have contributed an immense amount of data to our knowledge of the distribution of the cultivated Cucurbitas. Briefly, they have found that the greatest diversity of the group is found in Central Mexico, where *Cucurbita Pepo*, *C. moschata*, *C. mixta* (a variant of *C. moschata*), and *C. ficifolia* occur together under cultivation, in the same general area (Mesa Central). It is important to note the omission of *C. maxima* from the above list. Apparently this species has never been cultivated by the natives of Mexico, Central America, or the northern portions of South America.

Cucurbita ficifolia, according to the Russian investigators, is the most widely distributed species of the group. It is found in all countries from Mexico to Chile along the Cordillera. There are white-seeded and black-seeded forms; otherwise, the composition of the species is very stable over the entire range. *Cucurbita moschata* is almost as widely distributed as *C. ficifolia*. It is extensively grown in Mexico, Central America and Colombia, but does not extend southward to Peru and Chile. In Panama and Colombia it is the only cultivated species of *Cucurbita*. The forms found in Mexico and parts of Central America are typically white-seeded, while those of Panama and Colombia are brown-seeded. The Russians consider that the center of distribution of *C. Pepo* must lie to the north of the Mesa Central in Mexico, since it is completely absent from their South American collections, and appears only sparsely in their records from Central Mexico.

Parodi ('35) has made a significant contribution to the subject in his study of pre-Hispainic agriculture in Argentina. He finds that *Cucurbita maxima* was one of the principal species of plants cultivated by the Guarnies in northeast Argentina and Paraguay at the time of the conquest of the Rio de la Plata.

Cardenas ('44), after completing his studies of the cultivated Cucurbitas of Bolivia, comes to the conclusion that there were several varieties of *Cucurbita maxima* present in the Andean valleys of South America at the time of the conquest. On the other hand, *C. Pepo* and *C. moschata* are evidently of recent introduction into the cultivated crop complex of Bolivia, Paraguay and Argentina. He suggests that a thorough exploration of the temperate and tropical portions of Bolivia and Peru might uncover wild relatives of the cultivated cucurbits that would be helpful in deciphering their relationships. The basis for this suggestion is the discovery of a small, warted gourd (el "joko") in an isolated region of Bolivia (upper canyon of the Rio Caine). This gourd is cultivated for food and is believed to be closely related to *C. Pepo*.

SUMMARY

1. Negative evidence of the presence of *Cucurbita Pepo* and *C. maxima* in Europe prior to 1492, also familiarity of the herbalists of the 16th and 17th centuries with these species, suggest very strongly that they were introduced into Europe from the Americas.

2. An examination of the evidence in favor of the origin of the cultivated species of *Cucurbita* in the Old World indicates that it is very fragmentary, and in general unacceptable.

3. The botanical record, while not as extensive or decisive as it might be, clearly favors an American origin of the cultivated cucurbits.

4. Finally, the archaeological and botanical records lead inescapably to the conclusion that the four cultivated species of *Cucurbita, C. Pepo, C. moschata, C. maxima,* and *C. ficifolia,* are New World in origin. The possibility that *C. moschata* may have been common to both hemispheres is not ruled out, but it does seem relatively remote.

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Explanation of Plate

PLATE 11

Fig. 1. "Türckisch Cucumer" of Fuchs, apparently a variety of *Cucurbita Pepo.*

Fig. 2. "Meer Cucumer" of Fuchs, evidently *C. Pepo* var. "Small Sugar."

198
CVCVMIS TVR-
CICVS
Türckisch Cucumer.

1

699.
CVCVMER
MARINVS
Meer Cucumer.

2

1

Melo-pepones latiores Clypeiformes. T. 784.

2

Pepo maximus Indicus compressus. L. 365. T. 783.

3

4

5

Klein Indianisch eckechtig Peponen.
Pepo Indicus minor angulosus.

6

Explanation of Plate

PLATE 12

Fig. 1. *Cucurbita indica* from Matthiolus, probably *Cucurbita Pepo.*

Fig. 2. *Pepones lati* from Dodoens—*Cucurbita Pepo,* possibly var. "White Bush Scallop."

Fig. 3. *Cucurbita verrucosa* from Daléchamps, evidently a warted variety of *C. Pepo.*

Fig. 4. *Melo-pepones latiores Clypeiformes* from Lobelius, probably *Cucurbita Pepo* var. "Golden Custard."

Fig. 5. *Pepo maximus Indicus compressus* from Lobelius—the first illustration of *Cucurbita maxima.*

Fig. 6. *Pepo Indicus minor angulosus* of Tabernaemontanus, probably *Cucurbita Pepo* var. "Table Queen."

FOSSIL POLYPORES FROM IDAHO

HENRY N. ANDREWS
AND LEE W. LENZ

In June, 1946, we spent a day searching for fossil plant remains in the late Tertiary deposits in southwestern Idaho. Our primary quest in this region was for petrified evergreen cones that have occasionally turned up, although only in such quantity as to whet the appetite of collectors. The focal point of that day's collecting was approximately 10.5 miles south of Bruneau and .5 mile east of state highway No. 51 which runs south from Mountain Home, Idaho, through Owyhee County into Nevada. In the course of the day one member of our party, Mr. J. M. Dodds, a County Commissioner, of Boise, discovered a fine specimen of a petrified polypore. More recently, Mr. S. H. Osgood, of Rupert, Idaho, has sent us a fragment of another specimen. Although both of our specimens seem to be clearly referable to the fossil *Fomes idahoensis* Brown (Brown, '40), in view of the great rarity of fossil polypores a brief record of the specimens seems worth while.

This part of Idaho is well known to local mineral collectors for its abundance of fossil wood, as well as the occasional cones. Most of these fossils are weathering out of a loosely consolidated, fine white sandstone which is overlain by a brownish-buff sandstone of a harder texture likewise yielding petrified plant remains. Overlying the productive plant beds is a horizon which yields an abundance of well-preserved fish jaws (*Mylocyprinus robustus* Leidy). The only stratigraphical study of the beds in this region is that of Piper's ('24), and the horizon from which our fossils were obtained was apparently in his group No. 8 which is described as "Lake sediments, semi-consolidated, white, gray, and buff sandstones and sandy shales, volcanic ash; . . . .". These beds have been considered to be of Pliocene age although it is possible that they may be of later origin. In a recent letter (February 20, 1947) Dr. Bobb Schaeffer has informed us of a collection of *Mylocyprinus robustus* fossil fish pharyngeals in the American Museum that were collected "from an area in southwest Idaho between 'Catherine and Sinker Creeks.' This particular locality is considered to be Pleistocene and as this genus has not previously been reported from older formations I am wondering if your horizon might not also be referable to that period."

POLYPORACEAE

Fomes idahoensis Brown.—The Dodds specimen is a nearly complete sporophore, only a small portion of one side having been lost. As seen in top view (fig. 1) it measures 10 x 11 cm. It bears but one layer of pores, which are 12 to 15 mm. long and number approximately 720 per square cm. Judging from the portion remaining it did not attain a thickness exceeding 2 cm. The rings of growth, characteristic of the living bracket polypores, are clearly defined on the upper surface. While it is not sufficiently well preserved to reveal any significant

diagnostic characters, a longitudinal ground thin section reveals a fine filamentous structure suggesting mycelium. The specimen is preserved as No. 5000 in the collections of the Henry Shaw School of Botany.

The Osgood specimen (No. 5001) is a fragment of an appreciably larger polypore that was probably about 15 cm. in diameter. The pores of this specimen attain a length of slightly more than 20 mm.

The primary interest in these fossils lies in their evident position in the Polyporaceae, and within this family they appear to be most closely related to the genera *Fomes* and *Polyporus*. Their general aspect is that of a *Fomes*, and because of the close resemblance to *Fomes idahoensis* we have assigned them to that species. The lack of dependable color preservation in these, as in most fossils, detracts appreciably from making an entirely dependable comparison with modern species of *Fomes* and *Polyporus*. Brown has, however, noted a rather close similarity between *F. idahoensis* and the living *F. pinicola* (Sw.) Cooke.

Only two undoubted American fossil polypores have been recorded previously. Mason ('34) has described a specimen of *Fomes applanatus* (Pers.) Gill. from the Pleistocene Tomales formation of Tomales Bay, California. Brown's specimen of *Fomes idahoensis* was collected about 5 miles north of the Bruneau locality from which our specimens were found.

We wish to thank Mr. J. M. Dodds and Mr. S. H. Osgood for kindly presenting these fossil fungi for preservation in the Henry Shaw School of Botany collections. Thanks are also due Dr. Bobb Schaeffer, The American Museum of Natural History, for identifying the fossil fish pharyngeals as being referable to *Mylocyprinus* and probably the species *robustus* of Leidy. Through the courtesy of Dr. R. W. Brown we have been able to compare our specimens with a portion of the type specimen of *Fomes idahoensis*.

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Explanation of Plate

PLATE 13

Fomes idahoensis Brown

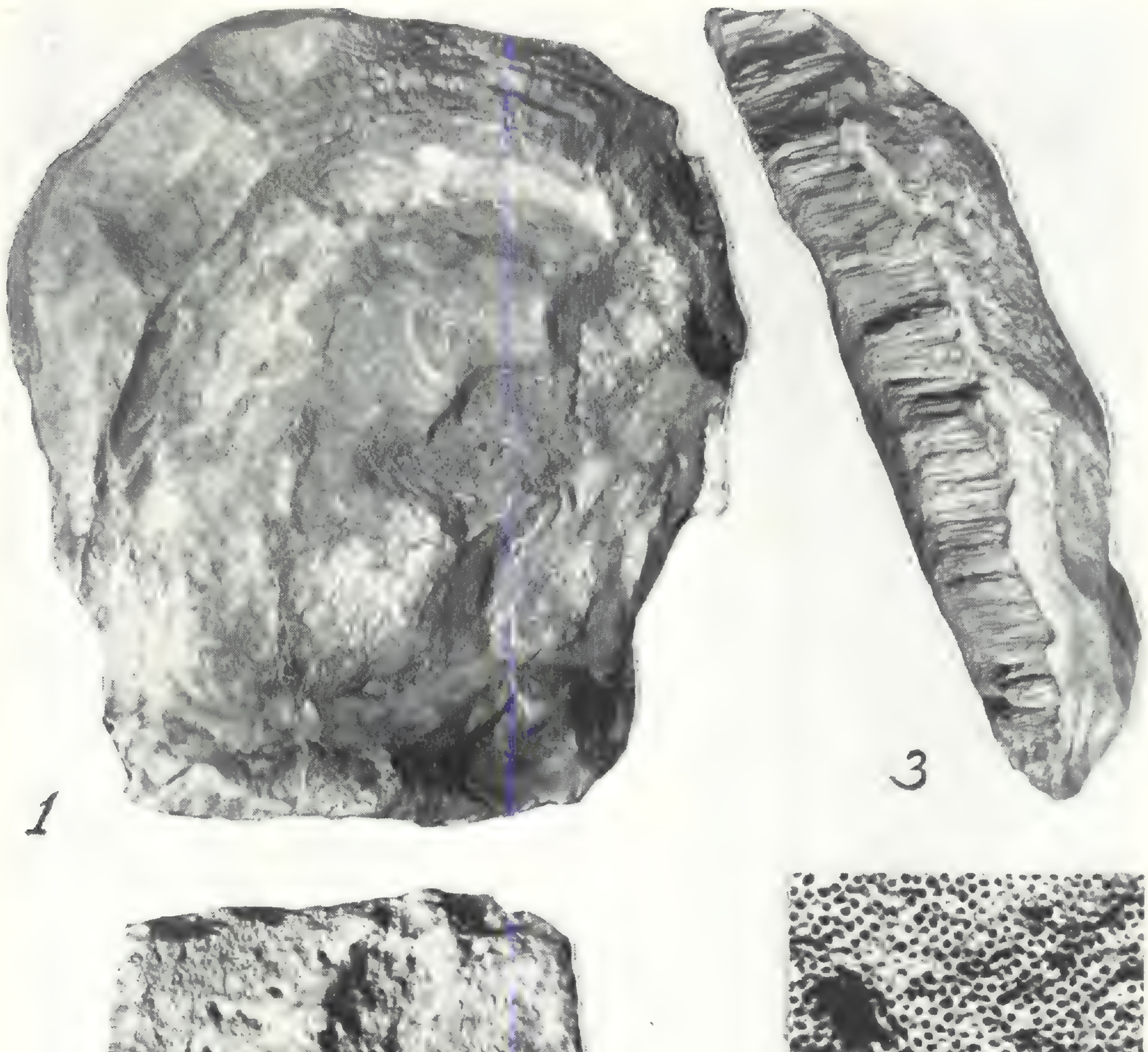
Fig. 1. Upper surface of the sporophore. Pores may be noted where portions of the context have broken away.

Fig. 2. Under surface.

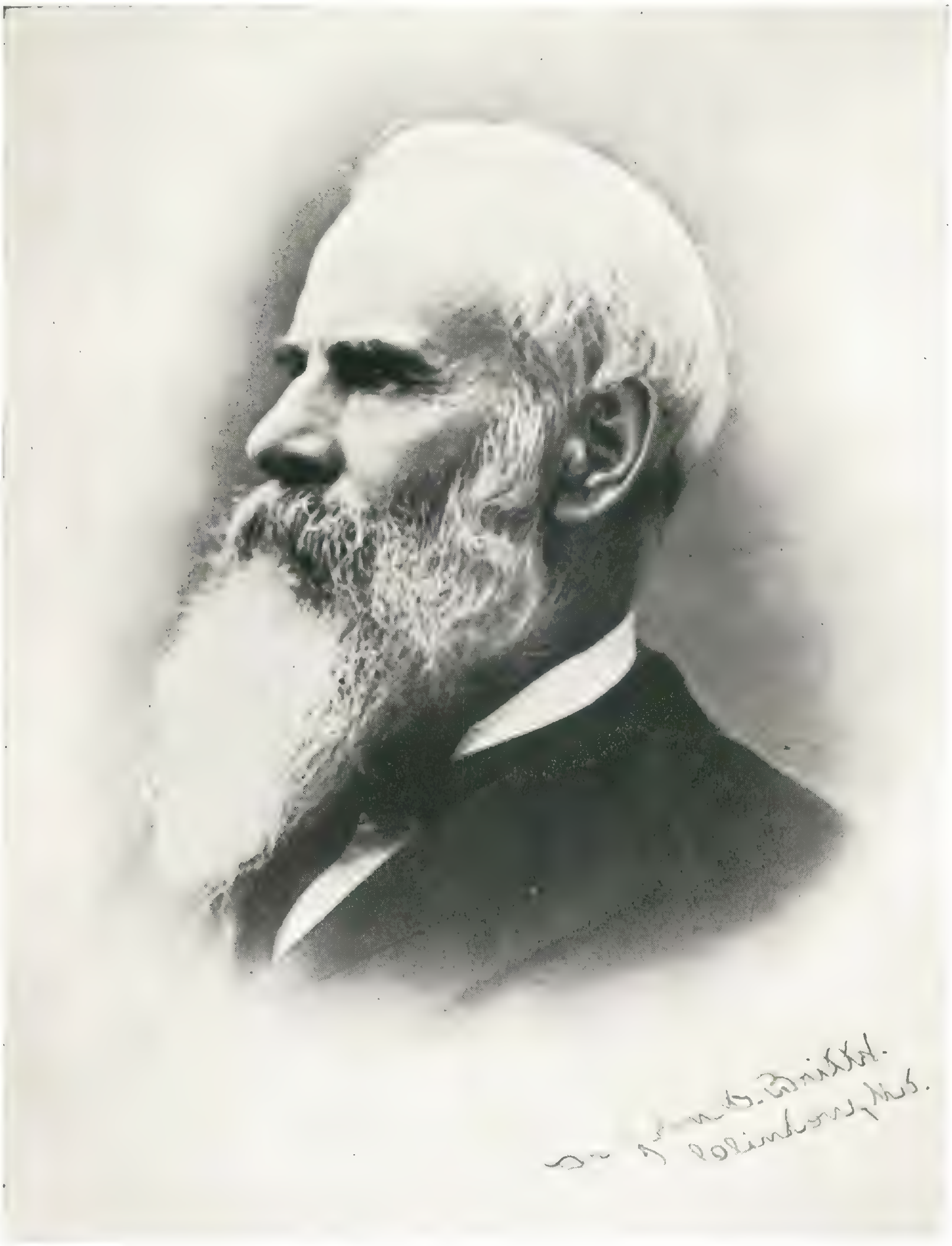
Fig. 3. Side view showing the single layer of pores.

Fig. 4. A portion of the under surface showing the pores enlarged.

Figures 1–3 nearly natural size. Figure 4 magnified 4 times. All photographs of specimen No. 5000.



ANDREWS & LENZ—FOMES IDAHOENSIS



DR. JOHN HENRY BRITTS

November 1, 1836—November 15, 1909

JOHN HENRY BRITTS—PHYSICIAN AND FOSSIL HUNTER

HENRY N. ANDREWS

In 1899 the United States Geological Survey published a classical volume on the Carboniferous fossil plants of the western Missouri region. The author of this work is the late David White, a noted and able geologist and paleobotanist, while behind the scenes, contributing the fossil plants that made it possible, worked a country physician of Clinton, Missouri, Dr. John Henry Britts.

The daily routine of Dr. Britts' life appears to have been no less crowded than is usual for men in his profession, although it was somewhat more colorful, judging from the variety and scope of his undertakings. In addition to his successful medical practice he found considerable time to serve the state in capacities of very lasting benefit. One of the most significant of these is the part he played in revealing the floral splendor of Missouri as it existed some 250 million years ago. But before mentioning in detail these more purely scientific achievements it may be well to briefly sketch in the background of his earlier life.

John Henry Britts was the eldest, and only son, of six children born to his parents, George Mathias Britts and Mary Jane Rogers Britts. His great-grandfather, Adam Britts, emigrated to this country from Germany about 1754, settled in Franklin County, Pennsylvania, and later moved to Virginia about the time of the Revolution. George M. Britts moved from Virginia with his parents apparently at about the turn of the 19th century and located at Ladoga, Indiana. He studied medicine and practiced in Parke and Montgomery counties until the year 1842. The son, John Henry Britts, was born November 1, 1836, in Montgomery County, Indiana. He attended the state schools until the age of 19, when he began the study of medicine. At that time he went to live with his maternal grandfather, Dr. Henry Rogers, with whom he remained until the spring of 1857, when he moved with his family to Clinton, Missouri. He then resumed his study under the preceptorship of his uncle, Dr. John A. Rogers, and during the college year 1857-58 attended lectures at the St. Louis Medical College. It is thus quite evident that he hailed from a family in which the medical tradition was well established, and in view of the scientific interests that he displayed through life it is not surprising that he followed this course at the outset. His formal training certainly was not extensive as compared with modern concepts, yet his learned relatives imparted to young Britts a sound and comprehensive scientific foundation, judging from the success and distinction that he later achieved.

Shortly after Dr. Britts began the practice of medicine in Cass County in 1859 Governor Jackson issued a call for troops to repel the Federal invasion of Missouri. Britts responded and proceeded to raise a company of which he was made Captain. Six months later he joined General Price's army at Springfield and helped to organize Waldo P. Johnson's battalion, which became later a part of the Fourth Infantry Regiment of the Confederate States Army. Dr. Britts was made surgeon of the

regiment with the rank of Major, later being promoted to Brigade Surgeon. On June 9, 1863, while on duty at the City Hospital during the siege of Vicksburg, he was wounded by a shell thrown into the city by Porter's fleet, and it was found necessary to amputate his right leg. The following August he left Vicksburg, a paroled prisoner, and after his recovery served as surgeon in Alabama and Georgia until the end of the War. Upon his return to Clinton in 1865 Dr. Britts formed a professional partnership with Dr. P. S. Jennings which lasted until the death of the latter thirty years later.

Dr. Britts' practice, like that of most physicians working in small cities and towns, extended over a wide territory. It was this frequent local travelling, combined with an intense scientific curiosity, that made possible the accumulation of his collections of fossil plants. At that time many coal mines were operating in Henry County and the adjacent territory, and Dr. Britts often visited them. Along with his medical kit, he always carried in his buggy a bag of tools, including pick and hammers, to carve out a few choice specimens from the shales that the coal miners laid aside for his study.

In addition to the numerous specimens that he furnished to private individuals and public institutions a large collection of Dr. Britts' fossils were placed many years ago in the Chicago Academy of Science's Museum. Mr. Eliot C. Williams, Jr., has kindly given me the following information concerning these specimens:

> "The accession record shows that on May 12, 1904, the Academy received a collection of 1124 coal plants collected by Dr. John H. Britts, in Missouri and Pennsylvania. This gift was made by Mr. Francis Peabody. A notation in the accession record states that the collection contains many types.
>
> "I have checked on the collection, and it seems to be in good shape, but I did not count to see whether or not there are still 1124. I would judge that the collection is probably intact.
>
> "A label in one of the cases indicates that this collection was the basis for Monograph #37 of the U. S. Geological Survey on the Fossil Flora of the Lower Coal Measures of Missouri, by David White." (Letter dated July 18, 1946.)

Dr. Roland W. Brown has informed me that the U. S. National Museum houses approximately 1,000 of Dr. Britts' specimens from the Missouri Coal Measures. Many of these are type and figured specimens. I have not had occasion to study these two important collections of American Carboniferous plants, although it is believed that paleobotanists working in this field would be glad to know of their whereabouts. Apparently the two collections contain all of the types in the above-mentioned Monograph.

Following the publication of the Missouri Monograph Dr. Britts continued collecting plants from the coal mines. Most of the specimens composing this later collection were acquired during or shortly prior to 1904. It was through the kind offices of Mr. D. K. Greger, formerly a curator of paleontology at Washington University, that the existence of this collection was brought to my attention some eight years ago. At that time it was in the possession of a grandson of Dr. Britts, Mr. J. B. Owen of Clinton, from whom it was later purchased for Washington University in St. Louis. It is not a large collection, but a considerable

portion of the specimens are of exquisite beauty both in their preservation and scientific and teaching value. It is especially rich in fine examples of *Asterophyllites* and *Annularia*.

Most of the mines from which these fossils were acquired have long since closed, and it is questionable whether it will ever again be possible to continue where Dr. Britts left off. At least we have a reasonably representative selection of the plant fossils from his old hunting grounds which will always serve as an invaluable foundation for such paleobotanical studies as may be carried on in that region. Our knowledge of Carboniferous floras is increasing every year as new regions are opened up and old ones reworked, and it is largely through the efforts of such active amateur workers that this knowledge is forthcoming.

Thanks are due Mr. John B. Owen for placing at my disposal biographical data pertaining to his grandfather.

THE IDAHO TEMPSKYAS AND ASSOCIATED FOSSIL PLANTS[1]

HENRY N. ANDREWS

AND ELLEN M. KERN

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HISTORICAL INTRODUCTION

Very few fossil plants have ever presented a more distinctive anatomy or more challenging problems than the Cretaceous Tempsykas. It is perhaps well to point out in these first few lines that we do not pretend to have arrived at a final accounting of all the existing gaps in our knowledge of these ferns. However, certain significant facts have been discovered concerning their habit and the plants associated with them in life which will stand unchallenged, while our interpretations may raise doubts or be modified by future investigations. It is intended that this should be taken as simply another chapter in our growing knowledge of the Tempskyas.

Through a most fortuitous circumstance that has been described elsewhere (Andrews, '47) I was able to comb certain of the hills in southeastern Idaho[2] in

[1] This study was aided by a grant from the Penrose Fund of the American Philosophical Society.

[2] Collecting activities were carried on by the senior author and certain persons in Idaho whose names are given in the Acknowledgments and elsewhere in this paper.

the early summer of 1942 under the guidance of Mr. W. A. Peters of Jerome, Idaho, chiefly in search of petrified trunks referred to the genus *Tempskya*. In a technical paper it may seem out of order to dwell on an introduction to the subject at hand, yet there are so many details of botanical, historical, as well as general human interest, attached to this group of plants that we believe they should be recorded for the benefit of those who may continue with studies of this and other plant groups in Idaho.

In the summer of 1939 I was presented with a small fragment of a *Tempskya* which had been collected in a gravel pile near the Haddenham fossil shop at Fossil, Wyoming. At that time even a fragment seemed like a treasure—it meant material for class study, but, of greater importance, it meant that Tempskyas should be found in much more abundance near by. In later years we traced the probable origin of that fragment to an Upper Cretaceous horizon running north and south a few miles to the east of Kemmerer, Wyoming. It was not, however, until an abundance of large, well-preserved specimens were found in the adjoining Idaho hills that we became fully aware of the importance of these plants in the Cretaceous vegetation.

Through an intimate knowledge of their countryside, a number of local collectors have enabled us to acquire a considerable quantity of specimens. The vigorous collecting activities of Mr. C. Henry Thomas, of Wayan, Idaho, and Mr. E. Manion, of Firth, should be noted in particular. Among the numerous westerners whose acquaintances have enriched my life and laboratory the name of Henry Thomas should be recorded as a great collector and a *Tempskya* specialist. In his assiduous search for these fossils he may be compared only with Wieland, who collected cycads in the Black Hills, or the early bone hunters such as Sternberg or Hatcher. It is a comparison on a smaller scale and of a somewhat more specialized nature, but the pioneering spirit and prodigious productivity differ but little.

My first contact with Mr. Thomas was in 1942, when he still occupied his former ranch on the Williamsburg bench area. I was not prepared to lunch in these rather remote though beautiful hills with a rancher whose cabin was lined with hundreds of books. While lacking the literary capacities of a Thoreau it was soon evident that here was a man who understood and appreciated the world he lived in. At the rear of Mr. Thomas's cabin a wooden platform already displayed scores of fine Tempskyas collected mostly within a radius of a few hundred yards. Encouraged by Dr. Roland W. Brown and myself, Mr. Thomas set to work scouring the near-by hills with increased interest and enthusiasm, with the result that the collection has been increased manyfold, consisting now of some few tons of fine specimens, in all probability far more than in all other collections combined (fig. 2). Believing that the Tempskyas are destined to occupy an important niche in Cretaceous floras, I requested Mr. Thomas to write in his own words a few lines pertaining to his discovery of the fossils in this region. This has been included in the Appendix for such historical interest as it may have for future paleobotanists.

THE PRESENT STATUS OF OUR KNOWLEDGE OF TEMPSKYA

Although petrified trunks belonging to the genus *Tempskya* were discovered well over a century ago in Europe, the first really informative accounts of these plants were those given by Kidston and Gwynne-Vaughan in 1911, and Seward in 1924. More recently Read and Brown ('37) and Read ('39) have given us much more comprehensive treatments. A detailed review of previous contributions is included in their account and will be repeated here only in so far as is necessary to orient the reader and to compare our findings and concepts with those of previous workers.

It is especially important to note that prior to Read and Brown's important work all descriptions had been based on either very poorly preserved specimens or a few fragmentary ones. The only possible exception to this statement is Seward's description of *Tempskya Knowltoni* from the Colorado shale of Montana. A detailed consideration of that specimen will be taken up later. This historical aspect of the subject is particularly significant in the case of *Tempskya* for its anatomy is so peculiar as to lead to highly erroneous conclusions concerning the habit of the plant unless adequate material is available for study.

Six species of *Tempskya* have now been described from North America. These include a specimen from Maryland described by Berry in 1911. According to more recent workers this was very poorly preserved and is of little interest or importance other than as a geographical record for the genus. Later Seward described his *T. Knowltoni* from Montana, and in 1937 Read and Brown described two more species and recorded specimens from a considerable number of localities in Wyoming, Idaho, Utah, Montana, and Oregon. Most recently Arnold ('45) has described two more species, *Tempskya Wesselii* and *T. wyomingensis*, from Montana and Oregon, and Wyoming, respectively. Combined with the previous European reports which record specimens from Russia, Bohemia, and England, the wide distribution of these plants in Upper Cretaceous times is well established.

We should like to emphasize that our own studies have not been primarily of a taxonomic nature. We are inclined to doubt that certain of the better-known American species are sufficiently distinct to warrant the specific names that they bear but with this phase of the *Tempskya* story we have no quarrel or primary interest. When dealing with anatomical characters it is not always possible to arrive at entirely satisfactory criteria for the segregation of species. In the rather large quantity of material that we have had available for study there is considerable variation in the gross form of the trunks, but with the exception of a very few specimens it has seemed most feasible to assign all of these to one species. Our efforts have been directed primarily toward arriving at a clearer concept of the general habit of the plants, their ontogenetic development and physiology. In pursuing this course we have perhaps tended to put less emphasis than previous workers on the segregation of species. However, in view of the undeniably close relationship of the species of *Tempskya* we do not feel that our approach has materially slighted a sound taxonomic treatment. While we have sectioned many

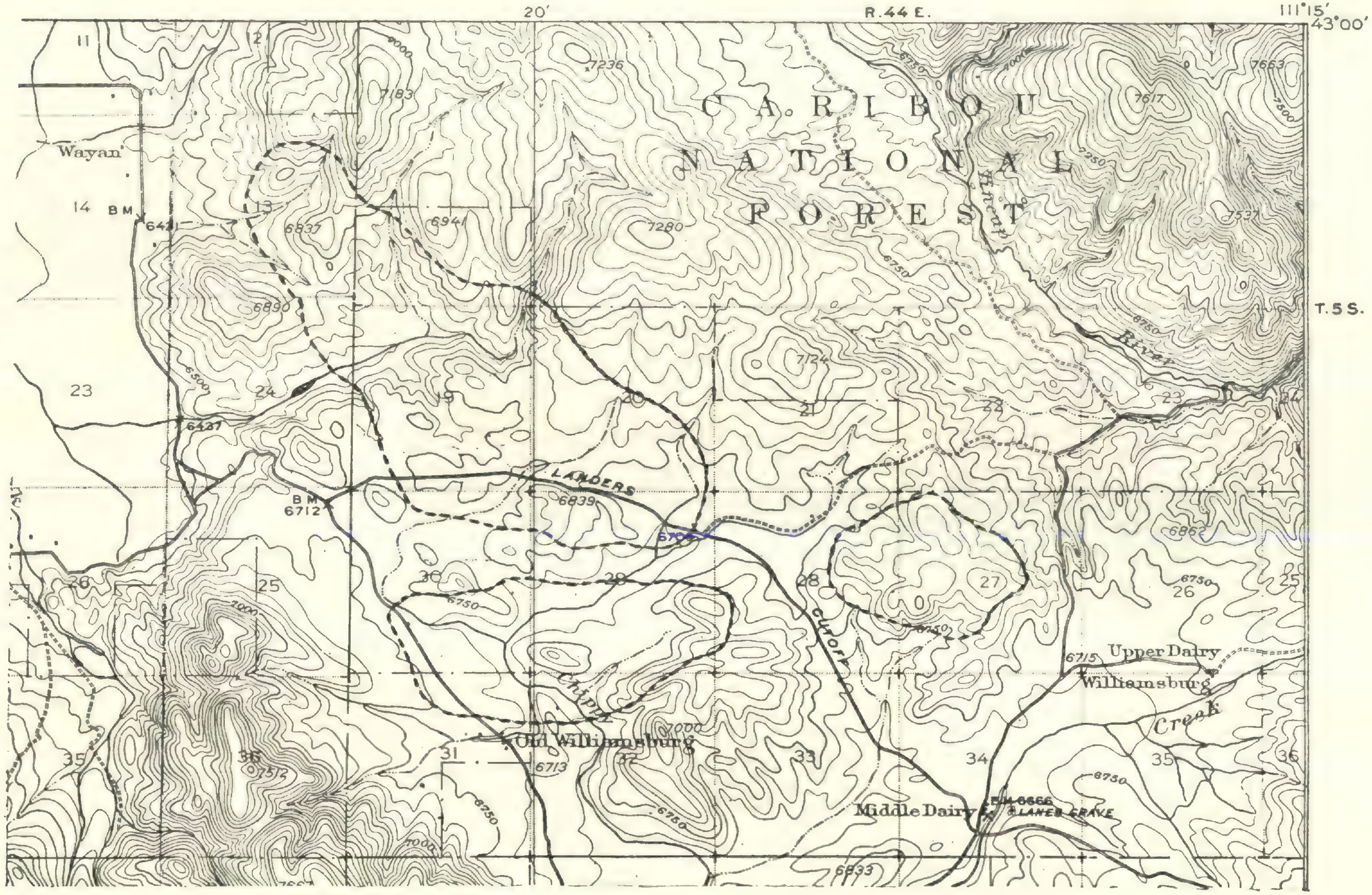
specimens through a wide variety of size and shape, a great many others, particularly the larger ones in the Thomas collection, have not been available for this purpose. We believe that we have studied in cellular detail an adequate number of representative specimens, and from scores of others we have drawn information concerning the habit of the plants. There is obviously some practical limit to the number of specimens that can be handled, and with some field experience with the Tempskyas one may select representative material with a minimum danger of missing essential details.

A typical transverse section of a *Tempskya* trunk reveals a most unique anatomy. It consists of numerous, small, siphonostelic stems held firmly together in a dense matrix of diarch roots (figs. 24, 28). Taken individually, the anatomy of a single stem is not unlike that of a modern maidenhair fern (figs. 20, 21, 22), such as *Adiantum pedatum*, while leaf traces are given off in two rows toward the nearest external point of the trunk (text-fig. 2). This unit aggregation of many branching stems with their petioles and roots has been called a "false-stem" by previous writers. It is, we feel, a superfluous term as well as somewhat misleading. If a special term must be used it would be more appropriate to call it a "super-stem," and while an adequately descriptive phrase would be cumbersome, we have preferred to use the term *trunk* as one that involves no new creation and can hardly be misinterpreted.

In order to define clearly the objectives in our own study it may be most expedient to note the chief gaps in our knowledge of these fossils. Sufficiently large collections had not been available for study to settle many of the concepts concerning the habit of the trunk—whether it was creeping, ascending, or upright. Read ('39) has discussed this in some detail in an interesting and critical paper. The ontogeny of the trunks, their unique physiological set-ups, and the manner in which the foliage was borne present problems that have been but partially explained. It is to these categories that we have been especially drawn. Furthermore, previous work on *Tempskya* has offered but little evidence of the kinds of plants that were associated with them in life. We have been fortunate in finding in the Wayan, Idaho, district the fossil wood of a conifer, a dicotyledon, as well as a cycad specimen with the silicified fern trunks.

THE LOCALITIES, AGE AND AREA

The greater part of the *Tempskya* specimens in our collection and all of those in the Thomas collection were obtained from an area of a few square miles immediately east of the Wayan post-office. In order to show this area precisely we have reproduced in text-fig. 1 the northeast corner of the United States Geological Survey's topographic map of the Lanes Creek quadrangle. Although the silicified trunks have been gathered over the greater part of this territory the most productive areas are shown within the dotted lines. Most of the collecting that has been done has been simply a matter of exploring the surface of the hillsides and small stream beds. Excellent material is obtained in this way, and in most cases the specimens show no evidence of long transport either before or after fossilization.



Text-fig. 1. The northeast corner of the Lanes Creek Quadrangle, Idaho, showing, in heavy dotted lines, the areas from which most of the *Tempskya* specimens have been collected in this region. Reproduced by permission of the United States Geological Survey.

During a week's collecting in the autumn of 1945 two days were spent excavating in section 27 in the bank of a draw from which Mr. Thomas had previously obtained some exceptionally fine material. Many of his largest and most complete trunks were obtained from a pit at this location. In the course of about three hours' digging one may expect to take out as many hundred pounds of specimens. However, with the exception of one other pit, very little digging has been attempted in this area. It seems likely that large quantities of the fossils remain underground.

This topographical area falls within the bounds of the Wayan formation although the exact position of the latter within the Cretaceous is still uncertain. The most detailed stratigraphical account of the region is that of Mansfield ('27) in which it is noted that "Definite correlation of the Wayan formation is impossible at present." In a chart showing the geographical distribution and stratigraphical correlation of *Tempskya* deposits in the United States, Read and Brown have tentatively placed the Wayan formation near the base of the Upper Cretaceous.

In 1942 Mr. E. Manion, of Firth, Idaho, kindly guided a small party of us to a hillside approximately 25 miles east of Ammon. The exact position of this locality is: NW¼ sec. 5, T. 2N, R. 41E, Hell Creek quadrangle, Idaho. Specimens have been found here in some abundance although the area is limited to a few acres in extent. The locality was revisited in 1946 and a dozen small specimens obtained. On that occasion we continued our search in the surrounding hills within a radius of two or three miles but found no other fossils. It is to be wondered that any one should have ever happened on this small outcrop, yet we feel that there must be many more in the vast extent of the Cretaceous beds that go far to the south. This locality lies approximately 35 miles northwest of Wayan and in all probability represents an extension of the same *Tempskya*-bearing beds. Specimens obtained here are generally well preserved although they do not differ anatomically from those collected near Wayan. This will be referred to as the "Ammon locality" in future references in this paper.

In Wyoming, shortly to the east, *Tempskya* is found in the Aspen shale and the Thermopolis shale, both of lower Upper Cretaceous age. *Tempskya Knowltoni* from Montana was found in the Colorado shale which extends into the middle Upper Cretaceous, while Berry's *T. Whitei* was derived from the Patapsco formation in Maryland, of upper Lower Cretaceous age. *T. Wesselii* (Arnold, '45) is reported from the Kootenai formation northwest of Great Falls, Montana (as well as a placer outwash at Greenhorn, Oregon). There is a possibility that the Montana specimens may have weathered out of the overlying Colorado group (Arnold, '45, p. 26). *T. wyomingensis* was found twenty miles northeast of Greybull, Wyoming. Arnold notes that "Fragments of *Tempskya* are widely scattered within the valley of Beaver Creek and its tributaries, but they are nowhere abundant. They have been found only where the Morrison formation is exposed and are associated with enormous numbers of dinosaur bone fragments and

gastroliths;".

It is thus clear that the Tempskyas ranged from the upper part of the Lower Cretaceous through middle Upper Cretaceous times.

SIZE AND FORM OF THE TRUNKS

With only one or two exceptions all the *Tempskya* specimens that we have examined from the Wayan and Ammon localities compare most closely with *Tempskya Wesselii* Arnold. Although the following discussion is based on this species unless otherwise noted, the views that are expressed concerning its habit, ontogeny, and physiology are probably generally applicable to the genus as a whole.

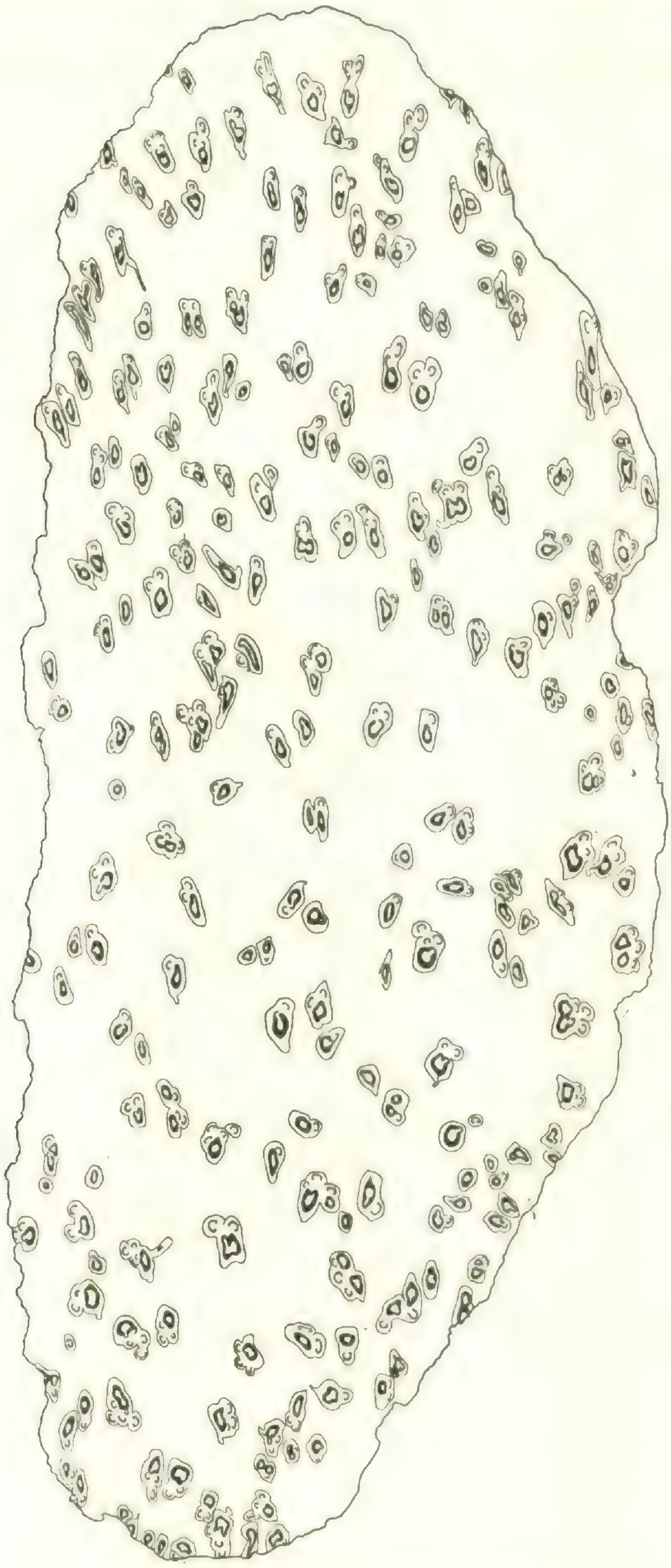
Some concept of the size that the Tempskyas attained was known as early as 1836 from Fitton's description of a trunk 9 feet long and 12 x 4 inches in diameter, found in the southeast of England (Stopes, '15, p. 14). Much more recently Read has reported trunks up to 10 inches in diameter. The largest specimen in the Thomas collection, and so far as we are aware the largest yet reported, is 16 inches in diameter. Other fragmentary specimens, which do not constitute complete transverse sections, indicate trunks of even larger size, so that a maximum of 18 or 20 inches in diameter seems very likely. It is thus clear that these were plants of no mean magnitude, although the evidence indicates that they did not attain a great height.

As a matter of convenience we shall consider the hundreds of specimens in the Thomas collection in three categories: basal specimens, tips, and intermediate portions which will be called *discs*. This latter term will apply to any specimen that is complete in transverse section but may be quite variable in length.

The bases.—One of the chief objectives of the 1945 trip to Wayan was to obtain basal portions of the trunks in order to shed further light on their general habit; that is, whether they were ascending or upright. Fortunately some fine specimens were collected in the field and others located in the Thomas collection. In all cases the specimens which we have interpreted as being the basal portions flare outward slightly at the very bottom (figs. 3, 5, 7), present a characteristic knobby lower surface, and are composed exclusively of roots. It is apparent, as Read and Brown have pointed out, that the stems in the older, basal portions of the trunks decayed completely, their place being taken by roots. A more detailed discussion of the anatomical details will be given later.

The basal periphery and under surface of these stumps are distinctive. The former is characterized by slightly buttressed, rounded projections and the latter by slightly raised knobs and cavities, or in a few instances by one large shallow cavity. The general uniformity of these specimens would seem to support the view that they represent the original stump portion of the trunk and not simply a broken sector taken from some higher level. It is pertinent to add, therefore, that they are all upright, indicating perfectly erect trunks.

One cannot be certain whether the roots extended out uniformly in all directions or whether they tended to aggregate into more massive "compound roots." The knobby character of the extreme base may point to the latter explanation



Text-fig. 2. A diagrammatic drawing of a transverse section of specimen T38 (peel 14) showing the distribution of the stems and the position of the xylem of stele and petiole traces. It may be noted that stem branchings are numerous and the trunk is radially symmetrical with respect to departure of the traces. Natural size.

although this is offered only as a suggestion. An objection may be raised that these small almost microscopic roots (pls. 20, 21, 24) could not have adequately anchored such a massive trunk. When it is considered, however, that they probably radiated out by the tens of thousands, that at some points they may have been aggregated to form compound roots, and that the individual roots possess an extremely stout sclerotic cortex (fig. 19, etc.), there can be no doubt that their supporting capacity was very great. Another objection may be raised that this knobby surface is an erosion artifact caused either before or after fossilization. However, the sides and upper surface of these specimens show no such effect, and the stumps always flare outward slightly at the extreme bottom, as might be expected.

The disc specimens.—The specimens that we have interpreted as being basal and terminal portions of trunks are considerably in the minority, which indicates that the plants did attain a height of at least some few feet.

If the cross-sectional form of these disc specimens could be depended upon as a specific taxonomic character the number of species represented would be very nearly endless. Different specimens vary from circular, to broadly elliptical, to strongly flattened in transverse section (figs. 10, 24, 25); and one specimen was found in which the trunk is crescent-shaped (fig. 9). Since we have not been able to observe any correlation between these variations in form and the internal structure of the trunks, such variations would seem to be of no taxonomic significance. It is possible that the variously flattened specimens have resulted from crushing caused by overlying sediments prior to silicification. A more detailed anatomical consideration bearing on this problem will be given on a later page.

The size and form variation of some specimens in the Thomas collection is recorded in Table I, this information having been compiled chiefly with the view of arriving at some concept of the height that these plants attained. In compiling these data a representative selection of specimens has been taken, all of which were complete in transverse section. Many more might have been added to the list, but in general they would have affected only the quantitative aspect of the table.

Since none of the specimens represents a complete trunk we cannot arrive at an exact figure for the height of a plant in life; however, from many observations of their diameters and the rate of tapering we may calculate a reasonably dependable minimum. In the cases of the base and disc specimens we have recorded the diameters at both ends in order to indicate the rate of taper. Of the terminal trunk specimens only the basal diameter can, of course, be given.

An examination of these figures for the trunk (disc) specimens will show that none of them taper abruptly from one end to the other. Such tapering is found only in the undoubted terminal specimens. The longest one that we have observed is in the Manion collection (specimen A), from the Ammon locality, and through its length of 21 inches it displays no tapering. The same holds true in a general way for the basal specimens, which flare slightly at the extreme base but otherwise give no evidence that the trunks were very short (figs. 3 and 7).

TABLE I
MEASUREMENTS OF A REPRESENTATIVE COLLECTION OF TEMPSKYA SPECIMENS

Specimen number*	Nature of specimen†	Diameter (s) in inches	Length in inches
9	Tr	9. x 6.5‡ 11. x 7.	12.3
11	Tr	9.3 x 6 10. x 7.	11.
19	Tr	11. x 10.‡‡	11.
21	Tr	12.3 x 10.5	6.
26	Tr	4.7 x 2.5 6. x 4.	11.
31	Tr	14. x 4.7	11.
32	Tr	8.5 x 6.5 9. x 7.	10.
33	Tr	10.5 x 5.	13.
38	Tr	5.5 x 3.7	6.
39	Tr	3. x 1.7 4.3 x 2.	7.
40	Tr	7. x 5. 8. x 5.5	7.
42	Tr	13. x 7.3	6.
45	Tr	8.7¶	11.
46	Tr	6.5 x 6.	10.
47	Tr	5. x 3.3 5.7 x 3.7	7.
48	Tr	9.3 x 5.3 10. x 5.3	9.
51	Tr. (near base)	14. 16.	10.
A (Manion coll.)	Tr	9.	21.5
W. U. (T216)	Tr	6. x 4.5 7. x 5.5	16.
6	B	7. 7.5	8.
10	B	8. x 5.5 9. x 7.	9.
13	B	11. x 7. 12.5 x 7.	9.
22	B	16.7 x 13.	8.
25	B	8.7 x 9.7 9. x 10.	7.
34	B	9.5 x 4. 9. x 6.	15.
41	B	9.7 x 7.3 8.7 x 7.3	10.
43	B	9.5 11.	9.
44	B	13. x 12.	12.
49	B	7. x 4.3 7.5 x 5.5	7.
23	Ti	8.5 x 13.¶¶	12.
24	Ti	10. x 4.5	7.
W. U. (T47)	Ti	6. x 3.7	8.5
W. U. (T230)	Ti	6. x 3.5	12.

* Specimen numbers refer to the author's field notes, all measurements being taken from specimens in the Thomas collection unless otherwise indicated. †Tr—trunk (disc); B—base; Ti—tip. ‡A slightly elliptical specimen, the figures in the upper and lower lines being for the top and bottom diameters respectively. ‡‡No appreciable taper of the specimen, the top and bottom diameters being the same. ¶No appreciable taper, and the specimen is cylindrical or nearly so. ¶¶In the case of tip specimens this refers to the diameter at the base.

In this respect it is necessary to consider the internal structure of the trunks. The densely compacted stems and roots that make up the trunks must have had in life the consistency of a very tough strand of rope. In texture it probably was not unlike an *Osmunda* rhizome with its vast coat of petioles and roots. In the *Tempskya* trunks, however, there were many stems and the whole aggregation was bound together very tightly. Thus while the trunks must have been very tough they were probably not extremely rigid. The thousands of roots created a closely interwoven unit; yet, lacking an interspersed ground tissue, such a height as is attained by a coconut or royal palm would seem to be improbable. One other pertinent point may, however, be mentioned here. Unlike other unbranched, columnar trees such as living palms, tree ferns, and cycads, *Tempskya* bore very small fronds, as is evidenced by the relatively minute size of the petioles, and we shall offer evidence that these were borne not merely in a crown at the top but for a considerable distance down the trunk as well. Thus, in all probability the Tempskyas did not have the mechanical problem of a large weight of foliage concentrated at the top, a feature which allows for a considerably taller trunk than might otherwise be expected.

It may be noted that some of the longest specimens from the Wayan region (Table I, Nos. 33, 34, T216) display but little tapering from one end to the other. The nineteen disc specimens considered in the table all have an average taper of approximately .6 inches per foot. Thus, assuming a uniform taper throughout, a trunk 10 inches in diameter at the base would taper to a point at a height of about 16 feet. This is probably in excess of the height actually attained since, among other factors, the apex of the trunk tapers abruptly to a blunt point (figs. 26, 27). From the terminal specimens at hand we may suppose, then, that at a diameter of 3 or 4 inches our trunk terminated, giving a height of about 12 feet. In view of the relative proportion of basal and terminal trunk specimens along with the discs this figure seems quite reasonable.

The specimen of maximum diameter (#51 in the table) measures 14 and 16 inches at the upper and lower ends, respectively, and is 10 inches long. This had been exposed for some time prior to collection and is somewhat lichen-encrusted. No evidence of stems could be observed in the transverse sections, indicating that the specimen came from near the base of a trunk, although it does not represent the basal-most portion as both end surfaces are irregularly broken. On the basis of the estimate given above for a trunk 10 inches in diameter it is possible that this specimen may represent a plant that attained a height of about 19 feet.

Prior to the publication of Read and Brown's work, accounts of *Tempskya* were based on so few, as well as fragmentary, specimens that a satisfactory concept of the habit of the trunks was not possible. Read has more recently presented a more detailed discussion ('39) dealing with "The evolution of habit in *Tempskya*." While certain of his concepts are clear-cut and sound, we are not able to agree in all respects with his conclusions. Read states, "In short, the writer's concept of the growth form of the dorsiventral false stemmed species of *Tempskya* is an as-

cending, climbing type of fern with numerous liana adaptations. It is of course obvious that the very basal portions of the stem were horizontal or oblique. However it is doubtful if these subterranean portions developed the dense mass of parallel roots characteristic of the false stem. Rather they must have been markedly divergent." (p. 70).

In the hundreds of specimens that we have collected or studied from the Idaho localities the evidence points toward an upright, self-supporting trunk without liana adaptations, and we cannot agree that it is "obvious" that the basal portions were horizontal or oblique. Our evidence as gained from a study of the external form of the trunks may be considered first.

It seems significant that we have encountered only two specimens (one shown in fig. 8) which show any noticeable longitudinal curvature. Basal specimens give no evidence of other than upright habit from the start.[3] Two concepts that seem to have become indelibly impressed in the minds of those paleobotanists who have seriously studied the Tempskyas deserve analysis at this point. The first of these is based on the specimen of *Tempskya Knowltoni* described from Montana by Seward in 1924. That specimen is described and figured as being 33.5 cm. long and obconical in form, the supposed basal end being 1.5 cm. in diameter and the enlarged apical end 6.5 in diameter. It is certainly apparent that a *Tempskya* trunk of such an obconical form would have been mechanically incapable of attaining any appreciable height, and even if it could in such a small specimen as this it must have been dangerously top-heavy. A very likely flaw, however, in Seward's interpretation of this as a complete trunk lies in the anatomy of the specimen. He has indicated (text-fig. 2, page 490) that the trunk is anatomically dorsiventral, that is, the petioles for the most part pass out toward one side. Read and Brown likewise figure *Tempskya minor* as showing predominantly dorsiventral orientation of the stems composing the trunk. We feel that it is very likely that these authors have been dealing, in such cases, with portions of much larger trunks in reaching these conclusions. By sectioning some 70 specimens and preparing peel preparations of the entire transverse surface we observed the course of the stems and petioles. These specimens have ranged from 5 to 30 cm. in diameter, and in nearly every case, whether the trunks were circular or oval in transverse section, the orientation of the stem-petiole organization with respect to the trunk as a whole is strictly radial,—that is, the petioles depart toward the nearest outer point of the trunk. This evidence of radial arrangement is based, furthermore, on trunk specimens that show no indication of appreciable weathering or fracturing. There can be no doubt that they represent complete transverse sections, with the exception of the outermost projecting stem tips and petiole bases. Seward indicates, moreover, that with his specimen "the surface appears to be waterworn." Evidence from a few specimens could thus be very misleading, and fragmentary ones must be expected

[3] In the earliest stages of the sporeling the first formed stem may have been creeping or ascending, but concerning this no information is available.

to display this apparent dorsiventrality. Specimens in our own collection, as well as many in the Thomas collection, would, individually, give this impression if complete transverse sections were not available for comparison. We do not wish to criticize Seward's very excellent anatomical study of the single specimen he had available, but rather we wish to point out the errors of interpretation that may readily result from conclusions based on such limited material. The over-all shape of his specimen also argues most strongly in favor of our view that it is but a fragment, for in all of the Idaho specimens the basal portions are clearly the largest in diameter and taper toward the apex. A more detailed consideration of this feature may best be saved for the following section dealing with the ontogeny of the trunk. (Also see discussion of the living *Dicksonia fibrosa* on page 145).

Bower has shown ('35, fig. 296, 1930, etc.) that in the ferns the young sporophytes are obconical in form, but it must be remembered that this is most apparent during the very early stages. Generally, the stelar system soon attains a maximum diameter as in most of the rhizomatous forms, or increase in diameter is rendered possible by polystely of one sort or another. The ferns have been remarkably adept at modifying their primary stelar tissues to make up for a lack of mastery of the cambium. Such rather divergent structural types as are represented by *Psaronius* and *Tempskya* illustrate the high state of organization that has been made possible. In the case of *Tempskya* we do not know what the very earliest stages in the development were like but there can be little doubt that maximum *individual stelar* size was soon attained and that stelar divisions started very soon after the sporeling stage. Perhaps during the first two or three feet of vertical growth the trunks were obconical, although it is most likely that root development soon counteracted this to produce a trunk that generally tapered from the base toward the apex.

The tips.—We have in our own collections three specimens of the terminal portions of trunks, all of which (figs. 26, 27) taper rather abruptly to a blunt apex.

THE ONTOGENY OF THE TRUNK AND THE RESTORATION

With the exception of the basal ones, characterized by their anatomical composition of roots and distinctive external features, all the specimens that we have examined display, in transverse section, stems scattered quite uniformly through them, from the extreme periphery to the center. Some specimens show considerably more stems per unit area, which is due, in part at least, to the position of the section, whether nearer the base or apex of the trunk. One of the most striking anatomical features is the short life span of the leaves. It is not possible to indicate precisely how long a frond persisted, but judging from modern ferns, cycads, and palms it probably was not more than one year. The evidence for this lies in the fact that petioles are found only in close proximity to the stem from which they were derived. Thus is would seem that any single stem must have been at the outside of the trunk, terminally or laterally, at the time it was bearing active petioles.

Previous workers have assumed that the *Tempskya* trunks bore a crown of fronds at the top in a fashion generally comparable with that of a modern tree

fern or cycad. The only previously figured restoration is that of Kidston and Gwynne-Vaughan's which appeared in Stopes ('15) Lower Greensand flora. In that restoration a ring of stems is shown composing a sort of compound crown at the top. They are shown branching two or three times, each with a rather dense cluster of leaves. From our observations, such a supposed habit is quite contrary to the evidence afforded by the internal structure of the trunks, as well as the external form of the tip specimens.

The tendency to compare these fossils with modern plants such as tree ferns and cycads is understandable. However, in *Tempskya* we are dealing with a different mode of increase in the diameter of the trunk, as well as a highly unique physiological set-up with regard to photosynthesis and transport of fluids. While most tree ferns, palms, and cycads bear a crown of relatively few, large leaves the Tempskyas bore a great many small ones, as is evinced by the minute size of the petiole (figs. 20, 28). It is evident from the dimensions of the petioles, by comparison with those of living ferns, that the fronds must have been very small, probably little more than a foot long. The physiological problem of light relationship where numerous relatively very small fronds are aggregated at the top of the trunk has not previously been given the consideration that we believe is necessary for a reasonable concept of the habit. A quantitative comparison with plants of supposed similar habit will clearly point out the difficulty.

We have measured the trunk and petiole diameters, as well as the number of leaves in a crown, for some cycads, palms, and a low-growing tree fern that are cultivated in the Missouri Botanical Garden greenhouses. The data are presented in Table II, together with those for a few representative specimens of *Tempskya Wesselii*. A comparison of these living columnar-trunked plants, with their crowns of leaves at the top, with the trunks of *Tempskya* reveals certain significant structural divergences. A wide range of trunk types has been purposely included, and of them we may immediately eliminate from close comparison those with tall and uniformly slender trunks and a few large leaves, such as the palms *Hexopetion mexicanum* and *Chamaedorea Tepejilote*. These plants are in no way comparable to the more massive trunks of *Tempskya*. The stouter-trunked forms such as *Phoenix reclinata*, and more especially *P. dactilifera*, present a closer structural comparison. The frond/trunk relationship is, however, worth careful consideration. Two specimens of *P. dactilifera* in our greenhouse measure about 12 and 14 feet high, respectively (up to the crown of leaves), and these have diameters of 14 and 16 inches, respectively, including the very heavy armor of leaf bases, the latter accounting for at least one-third of the trunk diameter. Of particular interest is the base of the petiole which tapers from 4 inches (in its wide diameter) close to the trunk to 1½ inches through a distance of 12 inches. A generally similar organization prevails in the larger-leaved cycads, the basal portion of the petioles being stoutly bulbous to support the weight of the leaf. In all cases we have prepared the petiole/trunk ratio from measurements of the petiole out beyond this

TABLE II

A COMPARISON OF CERTAIN MORPHOLOGICAL DATA IN LIVING PLANTS WITH SPECIMENS OF *T. WESSELII*

Living plants	Ratio of petiole diameter to trunk diameter	Number of leaves in a crown	Remarks
Cycas micholtzii	1:13	15	
C. circinalis	1:11	22	
C. siamensis	1:9	40	
C. revoluta	1:24	16	
Dioon spinulosum	1:9	40	
Encephalartos altensteinii	1:10	12	
Cibotium sp.	1:11		
Phoenix reclinata	1:4	27	Very little taper to trunk, which is enclosed in dense armor of leaf bases.
P. dactilifera	1:10	28	Trunk encased in very dense armor of leaf bases.
Hexopetion mexicanum	1:4	10	No appreciable change in diameter through its 10 feet of height.
Chamaedorea Tepejilote	1:3	4	Very slender clean trunk with little change in diameter through its 8 feet.
Thrinax parviflora	1:2.5	15	Gently tapering trunk, clean below with bulbous base 5″ in diameter which tapers to about 3″ at departure of first leaf.
Caryota urens	1:2.5	5	Trunk ensheathed with closely appressed leaf bases, uniformly tapering from 5″ at ground to 3″ where first leaf is given off at height of 6′.
Fossils			
Tempskya Wesselii specimens			
T18	1:30		
T33	1:63		
T51	1:48		
T90	1:39		

great basal swelling. Turning to the Tempskyas, in specimen T33 the mean trunk diameter is 170 mm. and the petiole diameter (taken immediately after the departure of the petiole from a stem) is 2.7 mm., the petiole/trunk ratio being 1:63. In comparison with a stout columnar cycad such as *Cycas siamensis* with a trunk 10 inches in diameter (including the leaf bases) and a height of 9 feet, with a petiole 2 inches in diameter close to the base we have a corresponding ratio of 1:5, or when the petiole diameter is taken out beyond the swollen base, a ratio of 1:9 as shown in the table.

The larger-leafed cycads and palms have, as might be expected, an exaggeration of this enlargement of the petiole base to support the weight of the fronds. The relative size of this bulbous base is noticeably smaller in the smaller-leafed species.

Since there is no evidence to indicate that the petioles of a *Tempskya* increased appreciably after their departure from the stem, they must have borne relatively very small fronds. The actual diameters of the petioles in a number of trunks of

T. Wesselii immediately after their departure from the stem varies from 1.5 to 2.75 mm. Dimensions of the petioles of cycads (taken immediately beyond the swollen base) range between 8 and 25 mm., those of *Cibotium* sp., 13 mm., and of the palms from 7 to 40 or more mm. Since these figures for the living plants are taken beyond the bulbous base, and the trunk diameters include the leaf base armor, the recorded divergence between their ratios and those of the Tempskyas is an extremely conservative one.

The Stopes restoration is ingenious in that it allows for a considerable proliferation of the leaf-bearing area. However, the actual terminal trunk specimens do not suggest any such appearance. All the specimens of this nature that we have observed, representative ones being shown in figs. 26 and 27, indicate a rather bluntly tapered apex like that of a living cycad, fern, or palm. In view of the generally good preservation of the Wayan Tempskyas, most of which show no great wear due to transport either before or after fossilization, we should expect to find some evidence of the stems or at least the rather massive stem aggregates as shown in the Stopes restoration. Such evidence is quite lacking.

A point that we wish to make is that the apex of a *Tempskya* probably could not have borne sufficient photosynthetic surface to have satisfied the requirements of the plant.

From the evidence afforded by internal structure, one of the most striking features of all *Tempskya* trunks (excluding the basal portions) lies in the fact that in any transverse section free petioles are rarely found more than a few millimeters beyond the stem that bore them. In other words (as previous authors have pointed out), the leaves were not persistent for any great length of time.

In order to arrive at a clearer understanding of the mode of lateral growth in *Tempskya* we have: first, observed the stem-petiole-root organization in transverse section in many trunk specimens, varying from approximately 2 to 10 inches in diameter; and, second, followed the course of individual stems in single specimens by means of serial sections. This latter procedure is considered in some detail in the following paragraph.

Two specimens, each approximately 4 inches in diameter,[4] were cut into a series of thin slices in order to determine the extent of branching in the individual stems, their destination, and the number of petioles that depart through a given length. The branching of the stems proved to be so frequent that the slices had to be taken between ¼ and ½ inch apart in order to follow them with certainty. With reference to stem branching, Read and Brown noted: "The writers attempted to determine the distance between these successive bifurcations by cutting a block several inches long into serial sections, but they found that this character is so variable that it has little value either for morphologic or for taxonomic considerations." (p. 110). While agreeing that the taxonomic value of stem branching

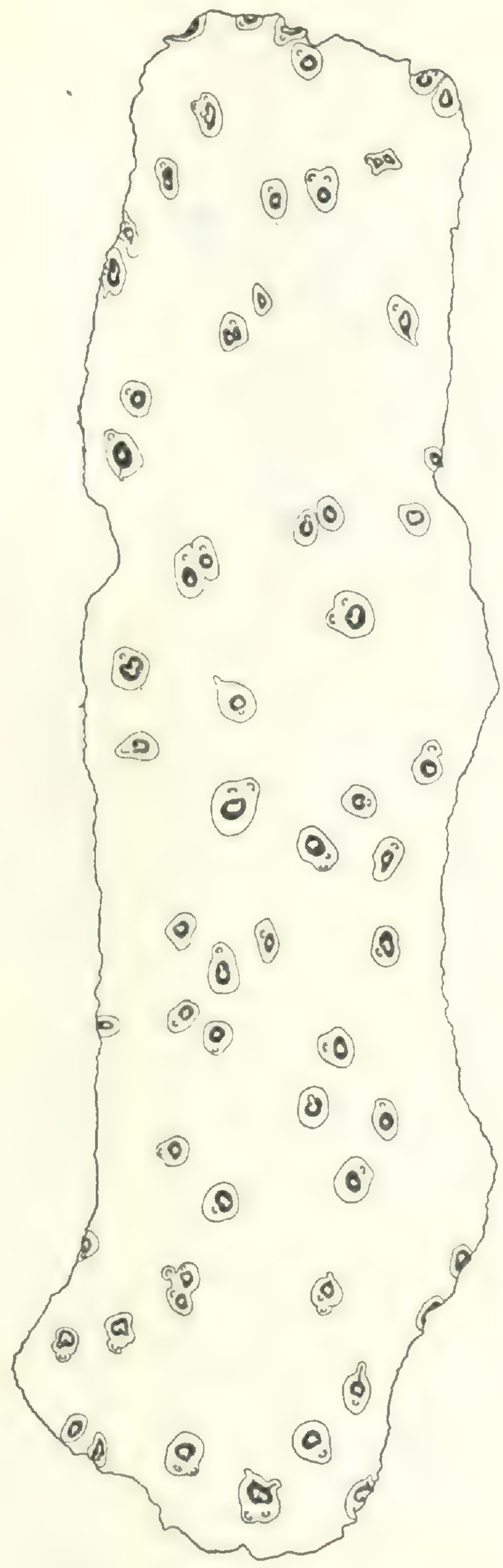
[4]Small specimens were selected for this purpose because of the extreme difficulty of cutting the larger trunks. From a comparison of many specimens varying in size from 2 to 12 inches in diameter there can be no doubt that the branching as described (based on specimens T51 and T90) is representative.

may be negligible we shall try to point out that it is of the utmost significance in an interpretation of the general habit and physiology of the plant as a whole.

It is evident, even without making serial sections, that branching of the stems is very profuse, for in almost any single transverse section of a complete trunk a considerable number of stems may be seen to be dividing. Taking more or less at random complete transverse sections from ten different specimens an average of 45 per cent of the stems was observed to be branching. Thus the serial sections, upon which text-fig. 3 is based, serve to confirm a three-dimensional picture that might have been prepared in a somewhat less exact fashion from a single transverse section. The worth of the peel method has proven an invaluable aid in anatomical studies of this sort. We have not relied upon it exclusively, but it is the only feasible way in which one can prepare complete sections, and often excellent ones, of trunks up to 10 and 12 inches in diameter.

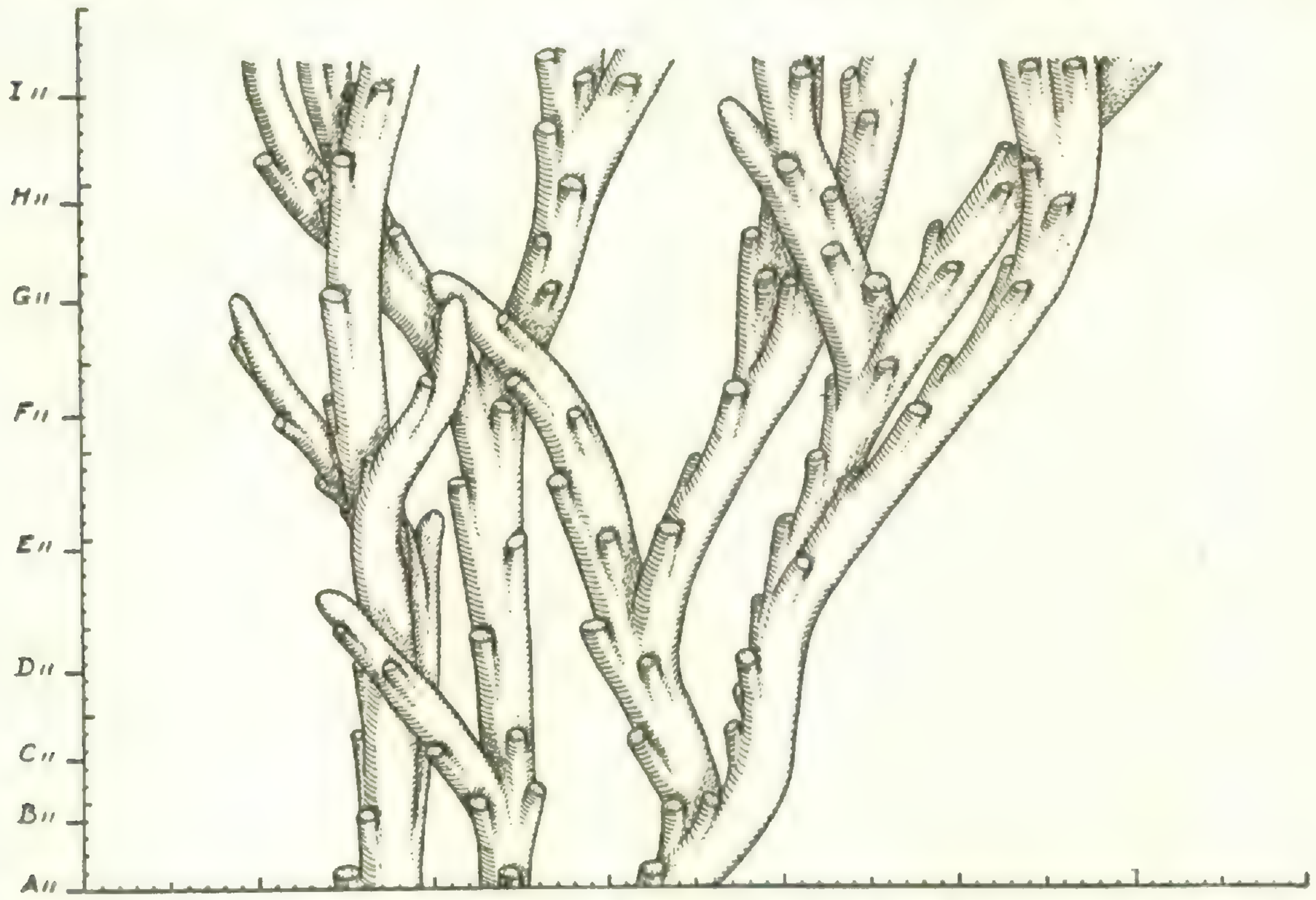
Previous accounts of the stem branching in *Tempskya* have indicated it as being dichotomous, and while this is predominantly the case it is not always so. In some specimens there may be appreciable variation in stem diameters as is shown in figs. 20, 21, and 22.

In order to present a three-dimensional aspect of stem branching we have selected several stems from specimen T90 which have been followed through a distance of 4.5 cm. (text-fig. 4). The average distance between successive divisions is approximately 1.5 cm. This abundant branching activity must result, through any appreciable distance, in either a great congestion of stems, or one of the two divisions soon ceases to grow. The latter is observed to be the case.



Text-fig. 3. A diagrammatic drawing of a transverse section of specimen T2 (peel 13) showing radial symmetry in the departure of the leaf traces in a strongly flattened specimen. Natural size.

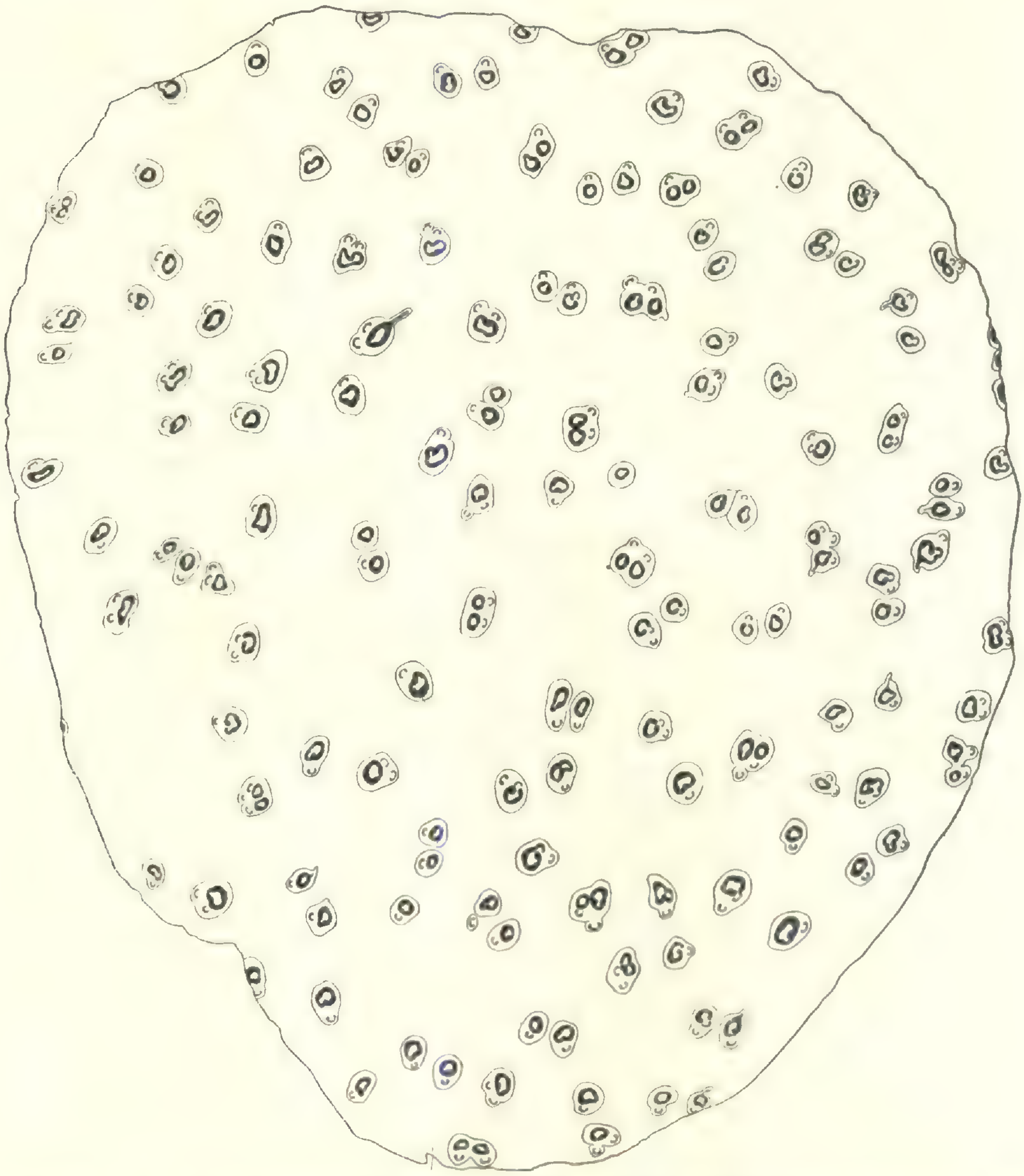
This frequent cessation of growth of many of the stems and the continued growth in the trunk as a whole, by the branches, present a distinctly different type of organization from that of other living or fossil plants with which *Tempskya* may be compared. In *Tempskya* the trunks increase in diameter as well as in height by this same process. While we cannot follow the growth stages of a single specimen in plants that lived 100 million years ago, we can arrive at an explanation of this developmental anatomy by observing trunks of varying sizes, and in all of them it seems clear that increase in diameter has taken place by the continued division of stems at the periphery of the trunk. In virtually every cross-section of a disc specimen stems may be observed (text-figs. 2, 3, 5) ac-



Text-fig. 4. A three-dimensional aspect of stem branching and the production of petioles as obtained by following the branches by means of serial sections, through a distance of 4.5 cm., of specimen T90. Each small division on the horizontal and vertical scales represents 1 mm. In their proper positions on the scale, letters to the left indicate the section, and numbers indicate the peel of that section used in constructing the illustration.

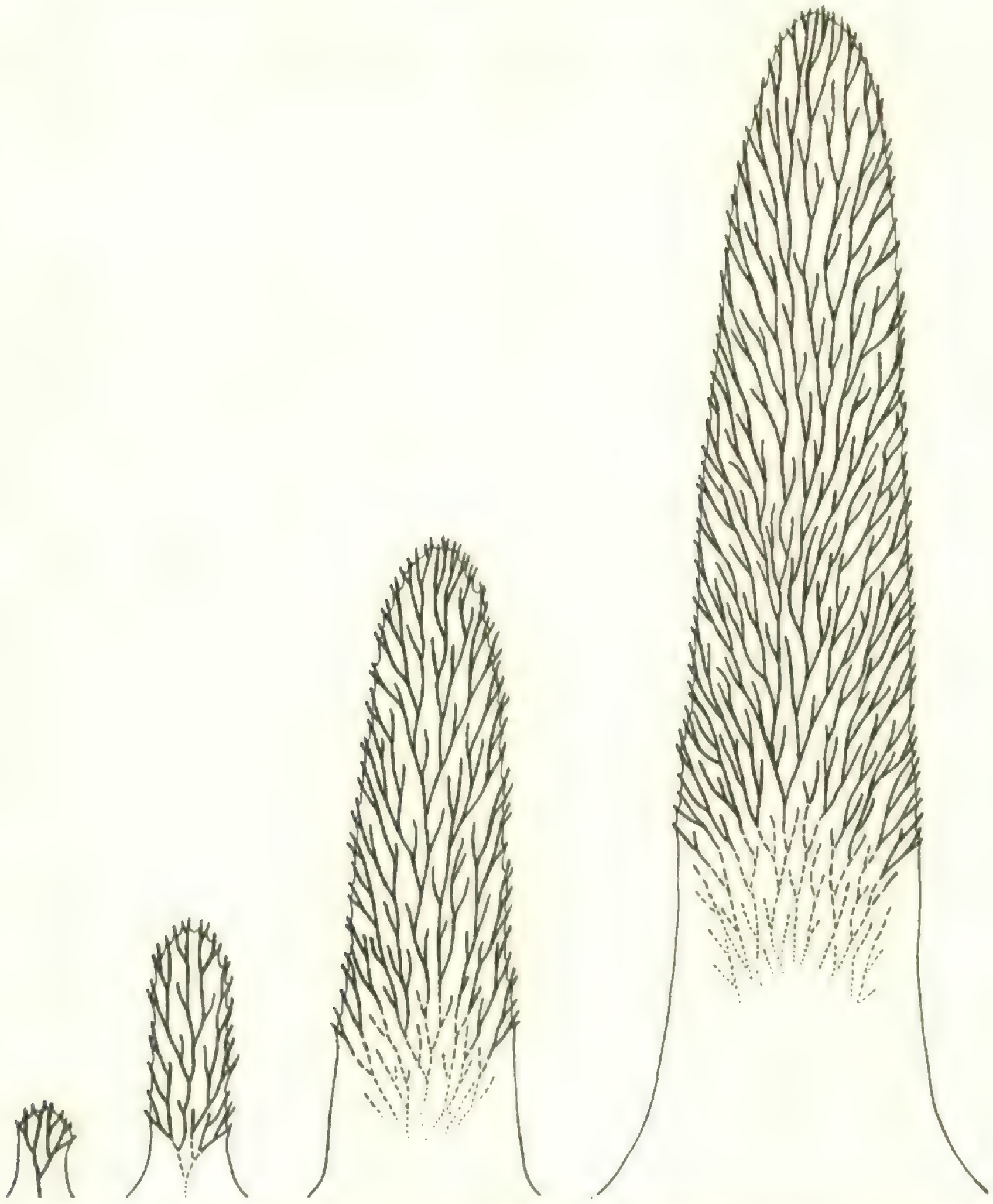
tually departing from the trunk. Just how far these projected out beyond the trunk proper cannot be determined as they apparently were readily broken off during transport prior to fossilization. It is difficult to observe these stems on the outside of the trunk because they departed obliquely and are not readily distinguishable from the roots either laterally along the trunk or at the tip. It is probable that they did not extend more than a centimeter or two at the most, as a greater length would have resulted in excessive crowding of the foliage.

After a short period of growth any individual stem divided, one branch ceased to grow, and the other carried on. We have attempted to show in the series of dia-



Text-fig. 5. A diagrammatic drawing of a transverse section of specimen T226 (peel 3) showing radial symmetry in the departure of the leaf traces in a cylindrical trunk. Natural size.

grams given in text-fig. 6 this apparent mode of growth. As stated above, we have no knowledge of the earliest development of the sporeling but it is evident from the smaller specimens that profuse branching of the stems was initiated very early in the development of the trunk. Just how long the original stems retained direct continuity with the ground likewise cannot be determined. The decay of the stems in the lowest portion was, of, course, gradual and the apical growth continued at a considerably faster pace. However, taking as an example a plant with a basal diameter of 10 inches and a height of 12 feet, it is probable that the lower 2 to 2.5 feet of the trunk was composed of roots (see extreme right diagram in text-fig. 6).



Text-fig. 6. A hypothetical series of longitudinal sections through *Tempskya* trunks showing the supposed mode of growth. The solid lines represent stems, and the dotted lines stems in various stages of decay.

In summary, these seemingly important points may be emphasized: The trunks had a generally tapering form from base to apex; branching of the stems was profuse and apparently uniform throughout the life of a plant, producing lateral as well as apical growth; leaves were not long-persistent and their small size would not have afforded sufficient photosynthetic surface as an apical crown alone.

Thus we feel that the *Tempskya* plants appeared in life as indicated in the accompanying restoration (text-fig. 7). While, as noted at the outset, this is based on specimens that we have assigned to *Tempskya Wesselii*, the close anatomical sim-

ilarity of all of the described species of the genus suggests a generally comparable habit. We wish to note that the kind of foliage borne by these plants is *not known*. Although the leaves shown in the restoration are of the *Anemia* type this does not necessarily imply such a relationship. They have been used to indicate rather the approximate *size and distribution of the foliar organs*.

THE ROOTS

The roots of the Tempskyas have been described by previous investigators including Kidston and Gwynne-Vaughan ('11), Seward ('24), Read and Brown ('37), and Arnold ('45). A rather close similarity of the anatomy of these organs has been noted in the descriptions of the various species, and we are in agreement with these previous workers in that the roots seem to offer no recognizable specific characters. There are, however, certain points pertaining to their physiology that seem deserving of further consideration.

If it is kept in mind that the basal portion of the trunk of the mature plant is composed entirely of roots, and the trunk at any point is composed largely of them, it is evident that they played a more than ordinary role in the absorbing, conducting, and supporting functions of the plant. A detailed study of these roots presents some rather challenging problems, and the literature of comparable physiological set-ups in living plants is by no means a copious one.

The roots, like the stems, branch profusely and present in any section considerable variation in size, degree of maturity, and preservation. The stele is small and, like the stem, consists only of primary wood. In well-preserved specimens (fig. 13) the phloem and endodermis are clearly defined. It is not often possible to identify positively any tissue that may be called the pericycle. In fig. 13 a thin crushed row of cells, apparently the pericycle, may be noted between the endodermis and the large metaxylem tracheid in the upper-right portion of the figure. Very early in the maturation of the extra-stelar tissues a conspicuous fibrous middle cortex is developed. This tissue is extremely variable, at times extending to the endodermis (fig. 13), and its development is accomplished to a considerable extent by abundant radial cell divisions which result in a distinctive tangential alignment of the cells (fig. 19). Taken by the thousands it is evident that such structures would develop a trunk of great strength—certainly not a brittle one—yet the close organization of roots suggests one of considerable rigidity. Without this sclerotic cortex is a rather broad, thin-walled outer cortex (figs. 11, 17), in most cases largely decayed, the outer remnants of it forming a collapsed loop which encloses the tissues.

Although the roots in general average a little less than 1 mm. in diameter there is considerable range in size. Within an area of a square centimeter roots may be found that are less than .5 mm. and others nearly 2 mm. in diameter. The smallest of these (mature) roots may have a middle cortex consisting of only two rows of the very thick-walled fibrous cells, a row or two of large, thinner-walled outer cortex, and epidermis.

The nature of the outer cortex may have some bearing on an interpretation of

Text-fig. 7. A restoration showing the probable habit of *Tempskya*, based on specimens of *T. Wesselii*. Foliage has not been found attached to the trunk. For further explanation see text.

the compressed forms in which the trunks often occur. It is evident that many of the roots in a normal trunk, prior to removal of the plant from its place of growth or fossilization, were largely decayed. Just how much decay did take place immediately before silicification cannot be determined and certainly varied with different specimens. Certain parts of specimen T53 are exceptionally well preserved, and within a small area (fig. 14) some of the roots still retain the most delicate tissues while intimately associated with them are others with nothing but the sclerotic cortex intact. Some of the former are young roots in which little thickening of the sclerotic cells had occurred and they show root hairs as well; the latter may be interpreted as older roots that had been dead for some time.

In contrast to fig. 14, the majority of sections show very few roots in which the outer, large, thin-walled parenchymatous tissue is preserved. Here and there a root may be in almost perfect preservation, and less occasionally a considerable group will be well preserved. Others have the inner cortex and stele intact and in still others the stele is missing, as well as the remnants of the outer cortical loop. Many of them reached this stage through death and decay during the normal life of the plant. If, however, any appreciable number of roots were alive and active at a given time (as must have been the case) a considerable percentage of the area of the transverse section was composed of this large, thin-walled, readily decayable tissue. It would seem, then, that the general decay of this tissue immediately prior to fossilization would have allowed even a relatively slight lateral pressure of overlying sediments to have compressed the trunks.

A comparison of circular and variously flattened specimens has been made in order to determine the mechanism of flattening. However, no differences were ever observed that might point positively to mechanical crushing. It may also be noted that in specimen T53, where the preservation of immature roots is so perfect, there is no marked indication of distortion. If we should assume that a large percentage of the roots was actively functioning and with their outer cortex intact the roots would have been so closely compacted as to have been strongly angular in shape. Yet where an appreciable number of roots happen to be well preserved in a small area (fig. 14) this is not the case. There is some compaction due to crowded growth but it is not excessive. It may also be noted that in most areas the roots, or remains of roots, are so crowded that there could not have been room for them all to have existed with their outer cortical tissues at one time. The evidence therefore indicates that only a portion of the roots composing a trunk was active at a given time. In this connection it may be noted that Schoute found very few live roots of the many composing the dense matrix of the trunk of *Hemitelia crenulata* (see page 144).

In his treatment of *Tempskya Knowltoni*, Seward ('24, p. 494) makes the following pertinent remark: "The contrast between the large number of roots without any visible connexion with their mother-organs and the small number of which the origin is demonstrated is remarkable. Most of them must have come from stems or leaf-bases that are unrepresented in the specimen."

Unfortunately, this evidence does not indicate positively whether the flattening of the trunks was natural or the result of the pressure of overlying sediments prior to fossilization. In summary we are inclined to believe, however, that the flattened form is not natural for the following reasons:

1. In any trunk there was, in life, a mixture of live, active roots as well as others in various stages of decay.

2. This organization allowed sufficient "inter-root-stem" space for the re-organization of these elements when crushed by overlying sediments without presenting a recognizable microscopic effect.

3. No other observable characters correlate with the wide range in transverse shape.

4. Circular and flattened trunks alike in our collection display a symmetry that is radial with reference to the departure of leaf traces.

5. It seems doubtful that a single species would have existed in such a wide range of forms.

Root hairs.—In many of our specimens we have been able to observe well-preserved root hairs, some of which are very long, as shown in fig. 12. These root hairs are often found on the larger roots which, judging from their size and general maturity, would seem to indicate at some appreciable distance back from the apical meristem. That these hairs occur on the older portions of the roots is, moreover, adequately attested by the fact that they may be observed on numerous roots within a small area. There can be no doubt that these are either persistent root hairs produced at an earlier growth stage of the root or that they are simply developed from the epidermal cells throughout the life of the root. There is evidence to indicate both modes of origin. The root shown in fig. 11 represents one of average size and certainly mature. Numerous short root hairs may be noted. These are complete hairs, as evidenced by the uniformly rounded tips, and not simply broken remnants.

In describing living specimens of *Dicksonia fibrosa* in New Zealand (see page 145) Field ('90) refers to the absorbing capacity of the aerial roots. In Tempskyas this function must have been of considerably greater importance than in most of the living ferns where the stem stelar system extends down to ground level. In the larger *Tempskya* trunks (10 to 12 inches in diameter) the stems had died away from the lower two feet, and possibly more, of the trunk. That portion of the trunk above this "root-stump" depended upon its water supply, then, either through the long slender roots reaching down from the stems or, more directly, through rain water absorbed from the apical and lateral surface of the trunk. There would seem to be little doubt that most of the minerals were taken up from the soil through the length of the trunk. However, the external surface of the trunk throughout must have been very absorbent and the trunk itself capable of retaining considerable moisture. The fact that deep within the trunk, roots are found with root hairs intact would seem to indicate that they functioned thus in drawing off this water reservoir.

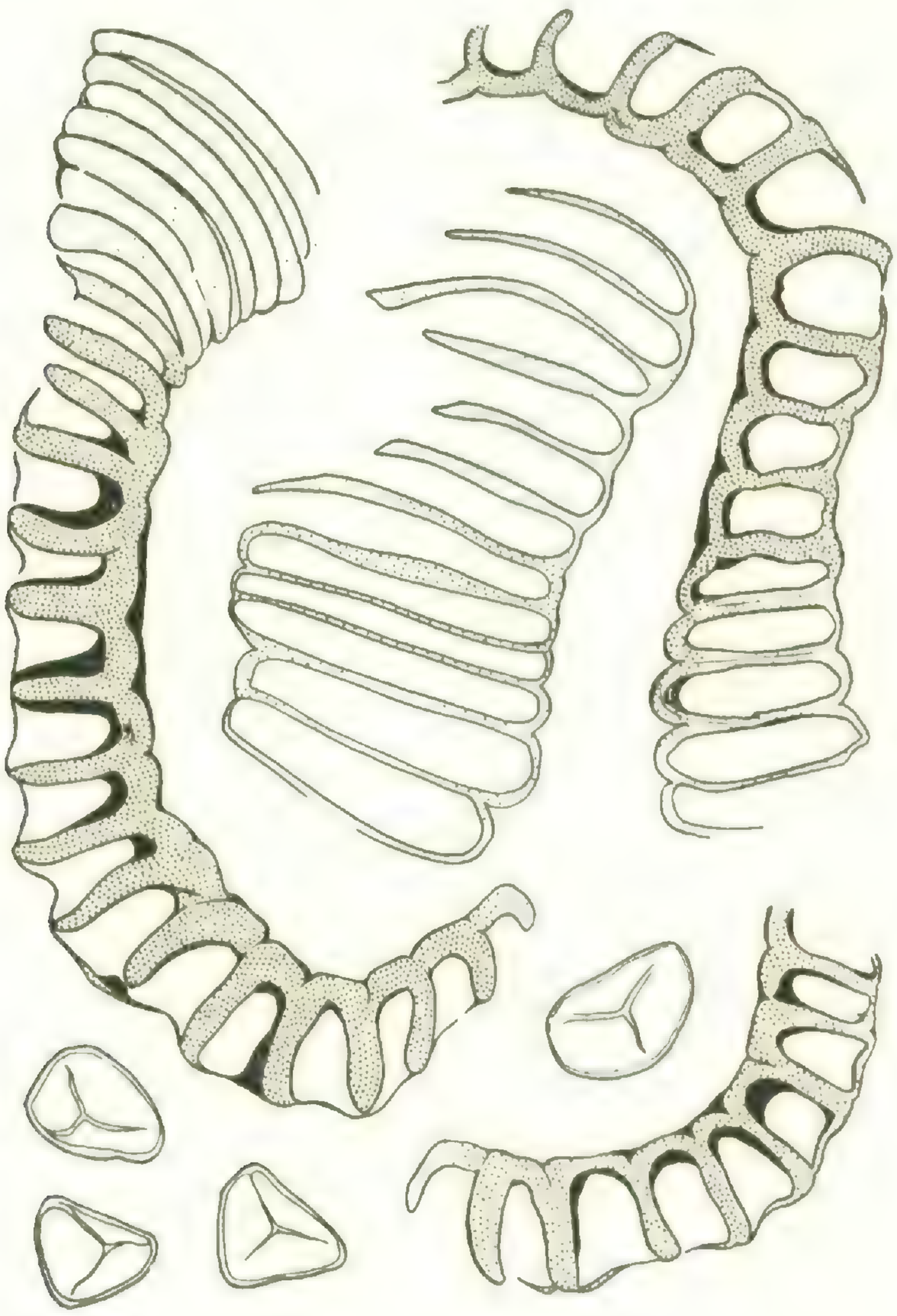
COMPARISONS WITH OTHER PLANTS, LIVING AND FOSSIL

The morphology of the trunk of *Tempskya* represents a peak of structural evolution along a line that is manifest in a generally comparable fashion in a number of ferns, both fossil and living. The ferns have developed some very remarkable and ingenious devices in the organization of their primary tissues to bring about increased size. Why they have never been successful in the use of a cambium is a mystery that we may never know, yet their other modes of development have been successful to a considerable degree and are none the less interesting. We have no reason to believe that any of the other plants mentioned below are closely related to *Tempskya*, yet they seem significant in offering clues to the racial origin of the Tempskya trunk (or "false-stem").

Scattered rather sparsely through the literature there are references to a number of living ferns having upright trunks composed of branching stems which are held together to a greater or less degree by a mass of adventitious roots. Since some of these references are extremely interesting, yet obscure and mentioned only briefly, if at all, by previous writers, a few of the most pertinent ones will be considered in some detail. In his "Ferns of New Zealand" H. C. Field ('90) presents a number of interesting accounts of ferns with stems of upright habit:

> "Rhizomes are of various kinds. The simplest form is that which grows 'erect' and produces its fronds in a crown or tuft at the top; in which case the plant is called a 'crowned' or 'tufted' one. In many ferns, this erect rhizome is prolonged above ground to a great height, as in tree ferns, and it is then called a 'caudex.' This caudex . . . is always clothed with fibrous rootlets by means of which moisture is imbibed from the atmosphere and helps the upward growth of the plant. The number of fronds which form the crown of the plant depends very much on the number of these aerial root fibres, our Dicksonia fibrosa, for instance, in which the actual caudex is only about two inches thick, while the fibres form a felted or interwoven mass, sometimes two feet in diameter, having often as many as forty fronds in its crown. Some caudices have a large conical base of root fibres; and in others this cone extends to the very top of the caudex, which is then of no great height, the whole mass being called a 'rootstock.' Sometimes an erect rhizome or caudex becomes flattened at the top and produces a great number of fronds, while at others it becomes divided into two or more branches, each of which produces a separate crown; and occasionally fresh crowns burst out of the side of a caudex. It is not quite certain how these originate. In some cases it appears to be the nature of the fern to divide itself in this fashion; in others, it seems as if young plants had grown on the face of a caudex; while in others it occurs by accident. I watched a case where a falling tree strained a supplejack tightly across the crown of a tree fern; with the result that the next spring the plant produced two crowns, one on each side of the supplejack, and thenceforth was forked. I have seen a cyathea dealbata with five branched caudices and crowns, and an aspidium aculeatum with seven, varying from three feet to five feet high." [pp. 11–12.]

From the point of view of comparison with *Tempskya* perhaps the most interesting of these extant New Zealand ferns is *Hemitelia Smithii*. This tree fern, which is known to attain a height of 20 to 30 feet, often divides at the tip into two or three branches. In 1886 Buchanan described a remarkable specimen from the slopes of Mount Cargill, near Dunedin. Buchanan's sketch of this tree-fern is reproduced in pl. 26. It is reported as being 16 feet high and with 16 branches and several buds. "The budding and branching may proceed from any part of the stem, and the specimen has several branches diverging in various directions, which again divide, as in dicotyledonous trees." According to the author's



Text-fig. 8. Spores and fragments of annuli found in a ground thin section made from specimen T16 (slide 1400). X 220.

brief description and figures, the branching is not dichotomous but rather "a branch is produced from a small bud, which pushes its way through the woody inner or true stem of the tree, and also the close fibrous outer covering." Shortly after the division of the single stele in the main trunk of this plant the resultant branches become separate as shown in the sketch. It thus differs from *Tempskya* in which the branches (except the extreme terminal portions) are permanently held together by the dense mass of roots. An interesting point of comparison, however, is that in *Hemitelia Smithii* the crowns of leaves on the respective branches are borne at different levels, thus differing from other tree ferns with "divided crowns," but not entirely unlike our concept of the mode of habit in *Tempskya*.

Another curious living fern is *Hemitelia crenulata* Mett., from the forests of Kandang Badak, Java, which was described by Schoute in 1906. It is a "tree fern"

(pl. 25) of considerable size, attaining a circumference of 201 cm. at 30 cm. above the ground. The basal two or three feet of the trunk consist of numerous branches enclosed in a dense matrix of roots, while above this the branches are free. Judging from Schoute's illustration of a specimen with a man standing beside it the plant attained a height of at least 12 to 15 feet. At ground level the trunk of *Hemitelia crenulata* contains but one stem while about 29 cm. above this it branches into three, while 28 cm. higher up seven branches are found. In the largest specimen reported, 33 branches are displayed which bear leaves in a crown as well as laterally. As may be noted, the branches grow horizontally out for a short distance and then ascend sharply.

The stem of *Todea barbara* Hook. f. seemingly presents an organization that is comparable to the above two ferns although we have been able to find but little information concerning the gross morphology of the trunk, most of the accounts dealing only with the cellular structure of individual stems, petioles, etc. Seward and Ford ('03) give the following account although it is not as pertinent to the present discussion as one might wish:

> "The stem of *Todea barbara* may reach considerable dimensions, forming a short and thick mass covered with a dense felt of brown roots, which completely hide the main bifurcated axis. One of the numerous plants of *T. barbara* sent to Europe by the late Sir Ferd. von Mueller has been figured, in which the stem reaches a breadth of 2.5 metres, a height of 1.76 m., and a thickness of 1 m. J. Smith also described a specimen from the Victorian Alps of Australia measuring 5 ft. 8 in. in height, with a diameter of 7 ft. 9 in., and weighing 1 ton 3 cwt.; he adds that a plant was received at Kew in 1869 weighing 15 cwt. and bearing 30 crowns and 160 fronds. The stem of a *Todea barbara* in the Cambridge Botanic Garden measures 8 ft. in circumference and 3 ft. in height, with 14 distinct 'crowns'; at the present time the crowns bear 230 fronds, with an average length of 7 ft. 6 in." [p. 239.]

From the large number of crowns that these *Todea* plants bear there must be rather profuse branching of the stems composing a trunk. Unfortunately, we know very little about this, for, as Sahni ('28) notes: "The mode of formation of the false stem still needs elucidation."

Field's ('90) account of *Dicksonia fibrosa* is also worth quoting. He writes:

> "The caudex seldom, if ever, attains the height of 25 ft., but is extremely stout in appearance owing to the mass of matted fibrous aerial roots which envelops the actual caudex and which is often 15 in. to 18 in. in diameter, and occasionally even more. Curiously enough, it is often larger in diameter above than below, particularly in plants not exceeding 6 ft. or so in height; which shows to how great an extent this fern absorbs nourishment from the atmosphere by means of its aerial roots."

This is the only case of obconical trunk shape, such as Seward reported for his single specimen of *Tempskya Knowltoni*, that we have come across in living ferns (other than in the very young stages). And, judging from Field's statement, it is not found in a completely mature plant. In view, then, of this data on living ferns and the fact that none of the hundreds of specimens of *Tempskya* from Idaho suggest such a trunk form it seems reasonably certain that Seward's specimen is either a very exceptional one or that it represents a fragment of a larger trunk.

The only fossil plant that seems to merit comparison with *Tempskya* is the Carboniferous zygopterid tree-fern from New South Wales described by Sahni

('28) as *Clepsydropsis australis*. Later, he ('32) gave reasons for its exclusion from that genus and proposed the name *Austroclepsis*. So far as we are aware its present valid name, then, is *Austroclepsis australis* (E. M. Osborn) Sahni.

It should be noted that there is no close genetic relationship between *A. australis* and the genus *Tempskya* for their individual stems and petioles have a strikingly divergent anatomy. Such resemblance as may be observed is only in the general habit of the trunks. In *A. australis* the petioles are large, almost equalling the stems in diameter; many petioles appear in a transverse section, indicating that they were long and the fronds persistent for some time; furthermore, the divisions of the stems are not nearly as profuse as in *Tempskya*. Thus the general appearance of *Austroclepsis* with its single crown of rather large fronds (Sahni, '32, text-fig. 14) must have been quite different from that of *Tempskya*. These two genera, widely separated in time and space as they were, possibly present in the gross organization of their trunks a similar evolutionary trend such as is exhibited in the above-mentioned living ferns, and it is a trend that probably took place independently in a number of different groups of ferns at different geologic times.

TAXONOMIC CONSIDERATIONS

As stated at the outset, our primary interest in this investigation was with the general habit, mode of growth, and physiology of the Tempskyas. A few points may be worth mentioning, however, in order to clarify our own taxonomic treatment as well as to offer suggestions that may be of use to future investigators. A careful identification of the specimens has, of course, been basic, and while we have assigned the name *Tempskya Wesselii* to most of our specimens other observers might find cause to split these into more than one species. Such "species" would be of very doubtful significance, and it seems certain that concepts pertaining to the life form and functions of the plants would stand unaltered.

Since the roots have presented no recognized taxonomic characters the identification of stump specimens can be made only to the genus. However, in view of their constant and uniform association with the trunk (disc) and tip specimens in the Wayan region there can be no doubt of their identity.

In view of the lack of evidence of natural affinities of the genus, Read and Brown ('37) created the family TEMPSKYACEAE, which constitutes the most expedient treatment. The only disappointment in our own investigation has been that such spores and sporangial fragments as were found in the trunks offer no positive help.

Prior to the work of Read and Brown eight species of *Tempskya* had been described: from Sussex, England; the basin of the Karaganda River in Russia; Bohemia; Maryland; and Montana. Many of these, because of their fragmentary nature and poor preservation, are certainly not worth further consideration and in their *Synopsis* Read and Brown have dealt with only two of them—*Tempskya rossica* Kidston & Gwynne-Vaughan from Russia, and *T. Knowltoni* Seward from Montana, and they have added two species, *Tempskya grandis* from Wyoming and

T. minor from Wyoming and Idaho.

More recently Arnold ('45) has described two more species: *T. wyomingensis* from "about twenty miles northeast of Greybull, Bighorn County, Wyoming, and *T. Wesselii* from Greenhorn, Oregon, and Great Falls, Montana.

Since it is perhaps most expedient to the present discussion we present the *Synopsis* of Read and Brown, to which we have added Arnold's two species in accordance with his concepts of their relationships.

SYNOPSIS*

1. Individual stems of false stem large, with very short internodes as indicated by the numerous leaf bases present in transverse sections. Xylem exarch or possibly slightly immersed in some specimens. False stem chiefly radially symmetrical. Xylem ring containing much parenchyma.
   - A. Inner cortex a broad zone of parenchyma containing near its inner margin an irregular but continuous tract of sclerenchyma. Outer layer of "pith" a similar zone of parenchyma, containing sclerenchyma, especially in the vicinity of the nodes..... *Tempskya grandis*
   - B. Inner cortex a narrow zone of large-celled parenchyma. Presence of an inner sclerotic layer not recorded..... *Tempskya rossica*
   - C. Inner cortex with two bands of stone cells. Smaller stems and longer internodes than the above two..... *Tempskya Wesselii*
   - D. Individual stems large (6–8 mm. in diameter), very close to *T. grandis*, differing chiefly in having a double layer of stone cells; internodes and stems larger than in *T. Wesselii*..... *Tempskya wyomingensis*
2. Individual stems of false stem small, internodes of such length as to permit only a little overlapping (2–3) of leaf bases. Xylem exarch. False stem dorsiventral. Xylem ring containing little, if any, parenchyma.
   - A. Xylem very compact; protoxylem commonly segregated into definite groups. Inner cortex broad, parenchymatous. Petioles common in false stems, indicating persistence of leaves; xylem arch, fairly flat. Stems averaging larger than those in the next group..... *Tempskya minor*
   - B. Xylem compact but with parenchyma in places interspersed with the tracheids. Inner cortex usually narrow, parenchymatous. Petioles rare in false stem; xylem arch, rounded..... *Tempskya Knowltoni*

*From: Read, C. B. and R. W. Brown: American Cretaceous ferns of the genus Tempskya. U. S. Geol. Survey Prof. Paper 186-F, p. 119. 1937, except parts C and D under 1, which have been abstracted from: Arnold, C. A.: Silicified plant remains from the Mesozoic and Tertiary of western North America. Mich. Acad. Sci., Arts, and Letters **30**:24–33.

Read and Brown have considered the gross organization of the trunks, that is whether radially or dorsiventrally symmetrical, of importance, while Arnold places considerable weight on the structure of the cortex in the delimitation of species.

In almost all cases where it is certain that we are dealing with complete transverse sections the symmetry of the trunks is essentially radial. In order to present some quantitative evidence of this we have taken a representative sampling of specimens displaying different shapes and noted the direction of departure of the petioles (Table III). These show quite clearly that the departure of the petioles is usually toward the nearest periphery of the trunk, as shown in text-figs. 2 and 5. It is not surprising that an occasional stem should bear its leaves toward the center rather than the periphery of the trunk but this does not necessarily point toward

TABLE III

COMPILATION, FROM A REPRESENTATIVE SELECTION OF SPECIMENS, OF STEMS, CONTRIBUTING TO RADIAL OR DORSIVENTRAL SYMMETRY OF THE TRUNKS, THE FORMER BEING STEMS IN WHICH THE PETIOLES PASS TOWARD THE NEAREST PERIPHERY OF THE TRUNK, THE LATTER THOSE WHICH ARE IRREGULAR IN THIS RESPECT

Specimen and peel number	Shape and dimensions in transverse section (inches)*	Total number of stems	Ratio of dorsi-ventral to radially symmetrical stems	Percentage of stems contributing to radial symmetry
T205, B1	E 3 x 2	57	1:50	98
T2, T5	E 5¾ x 1½	50	3:38	95
T47, T19	E 5¾ x 3½	134	0:114	100
T3, T3	E 3½ x 2½	68	5:58	92
T90, AT8	E 3½ x 2½	67	3:54	95
T51, GB T1	T 4 x 3	74	5:56	92
T201, A1	E 2¾ x 2	53	3:47	94
T202, B1	T 3 x 1½	27	2:23	92
T5, T2	C 2½	20	2:18	90
T4, T1	E 3½ x 2¾	70	1:55	98
T17, T3	C 2¾	52	7:47	87
T53, T3	E 6¼ x 2½	96	1:81	99
T45, T5	E 3¾ x 3	60	6:48	89
T42, T7	E 4 x 3½	68	5:58	92
T33, T7	E 7¾ x 4	158	3:122	98

*E, elliptical in transverse section; T, triangular; C, circular. The stems in the central third (diameter) of the trunks have been omitted since these are more variable in the direction of departure of the petioles and represent for the most part the terminal stems of the trunk.

asymmetry of the trunk as a whole. Since the stems probably projected out a short distance beyond the trunk proper it is quite conceivable that they could have given off leaves on the inner as well as the outer side.

In only one of our specimens is there a tendency for the petioles to pass predominantly in one direction. This is a small specimen, or quite possibly a portion of a larger one. It must be admitted that while our own observations are based on a large number and variety of specimens their geographical distribution is not great. We feel inclined to predict, however, that when comparable collections are gathered from other regions and when it is certain that the individual specimens are complete in transverse section, they will reveal radially symmetrical trunks.

With respect to the anatomy of the cortex, we have noted under the "Techniques" section differences that may be encountered in a study of identical stems of a trunk using peel preparations *vs.* ground thin sections. Also important is the variation in this character (particularly the apparent presence or absence of the stone cell band on the inside and outside of the inner cortex) that may show up in consecutive peels taken from the same specimen. With the proper etching time the sclerotic bands stand out in striking contrast to the parenchymatous tissue; but where the time is too little or too great the contrast may be much less apparent, or even barely discernible.

These differences are pointed out as neither an indictment against the methods themselves or the results of previous workers but to show that there are two points of the utmost importance in studying the genus *Tempskya:*

1. Specimens displaying complete or nearly complete transverse sections of the trunk are absolutely essential to taxonomic and morphologic studies.

2. Great caution must be exercised in delimiting species with reference to the way in which sections are prepared.

We feel that our own investigation has shown the probable lack of taxonomic significance in the gross symmetry of the trunks as used in the preceding synopsis. Furthermore, in view of the rather close gradation of the other characters that have been used to delimit species, as well as the fact that some have been based on rather scanty material, there is considerable doubt whether *Tempskya minor*, *T. Knowltoni*, *T. Wesselii*, and *T. wyomingensis* represent distinct species. We do not wish to carry this taxonomic problem further but as our knowledge of *Tempskya* grows it is likely that rather extensive revisions will be necessary.

Spores and sporangia.—In 1895 Boodle described some spores that he found in a specimen of *Tempskya* identified as *T. Schimperi*, collected near Brightstone in the Isle of Wight. These are 65 μ in diameter and "spherical or oval to bluntly tetrahedral," with a spore wall conspicuously sculptured with long bars. He noted a close comparison of these spores with those of the living *Anemia elegans* (Schizaeaceae), although he also points out that *Ceratopteris thalictroides* (Parkeriaceae) has spores with a similar sculpturing.

Seward found in his specimen of *T. Knowltoni* structures which appear to be the annuli of a Schizaeaceous fern, and probably belong to the genus *Anemia*. It is largely on account of these reproductive organs that *Tempskya* has been thought to be of Schizaeaceous affinities.

The only contribution that we have been able to make in this direction perhaps confuses the picture more than it helps to clarify it. Ground thin sections of two of our specimens (T16 and T3) contain considerable numbers of spores and fragments of the annuli of fern sporangia. The spores occur as isolated individuals, as well as aggregations of about 100 to 200, and in all cases the exine appears quite smooth. They are mostly collapsed, but a few appear triangular to slightly elongate (text-fig. 10 and fig. 23), these averaging about 50 x 40 μ. The spore shown in fig. 23 measures 51 x 36 μ.

The lack of any sculpturing of the spore wall and the occurrence of spores in large masses might lead one to infer that they are simply immature. However, since the exine is smooth in all of them, and an appreciable number is scattered about as individuals, it is probable that this is a mature character. For whatever the comparisons are worth it may be pointed out that there is a general lack of surface ornamentation throughout the genus *Gleichenia* (Gleicheniaceae), while *Thyrsopteris elegans* (Dicksoniaceae) has spores that are likewise smooth-walled (Knox, '39) and compare closely with our fossils.

Associated with these spores are some annulus fragments (text-fig. 10). Speculations on these fragments can lead to no definite conclusions although it seems clear that they are not Schizaeaceous, nor is it likely that they represent the

Osmundaceae or Gleicheniaceae. A much closer comparison seems to be afforded by the modern Polypodiaceae or possibly the Cyatheaceae-Dicksoniaceae.

We have chosen to refer our specimens to *T. Wesselii* Arnold because they compare most closely with the published description of that species. For those who may be especially interested in *Tempskya*, as well as for the purposes of record, we have compiled short descriptions of a representative selection of specimens of *T. Wesselii* in our own collections, pointing out especially distinctive characters that the respective specimens present:

Specimen T33.—A disc specimen measuring nearly 8 x 4½ inches in transverse section and 6 inches long. This seems to be representative of the larger, flattened trunks. Approximately 160 stems are found in a single transverse section, of which about 74 are shown in various stages of branching. The individual stems average 3.5 mm. in diameter, most of them being fairly close to this figure, although a maximum variation of from 1.5 mm. to 5 mm. in diameter may be found. The steles in the peripheral inch of the trunk are, for the most part, appreciably better preserved than those deeper within. Such differentiation of preservation is not as noticeable in the smaller specimens.

Specimen T2.—A much-flattened tip specimen (fig. 26 and text-fig. 3) approximately 6½ x 1½ inches in diameter and 2¾ inches long. Of the 57 stems shown in transverse section 18 are branching. The stems average 3.5 mm. in diameter, with a maximum variation of 2 to 4 mm. The preservation is uniform throughout the specimen, as might be expected in a small trunk tip.

Specimen T53.—A flattened, nearly oblong-shaped disc measuring 6½ x 2½ inches in transverse section and 2½ inches long. This is unusual only in the mode of preservation, the smoothed surface (and peels) presenting a characteristic blotched appearance due to the irregular quality of preservation.

Specimen T47.—A somewhat flattened tip specimen 9 inches long, in which a transverse section 5 inches from the top measures 6 x 3½ inches. Of the 134 stems in one transverse section, 45 are shown in various stages of dichotomizing. Each stem is giving off petioles toward the nearest point on the periphery of the trunk, thus producing perfect radial symmetry. Stems in the central part of the trunk are shown in perfect transverse section in any peel preparation, whereas those toward the periphery are shown, in the same peel, in somewhat oblique section, indicating that the stems at the edge of the root mass bend slightly outward while those in the center of the trunk keep a more or less vertical course.

Specimen T216.—A disc specimen 13 inches long which is somewhat triangular in transverse section. The transverse section at the bottom of the specimen measures 6¾ x 5¼ inches, while at the top it measures 6 x 4½ inches. Several hundred stems are present in a single transverse section, the radial arrangement of which is apparent.

Specimen T27.—A very much flattened, small disc specimen from Mr. Thomas's collection, about 4½ inches long and measuring about 3½ x ⅞ inches

in transverse section at the top. At that point only eight stems are present in the transverse section, and all but one of these are in some stage of branching. The stems average 2½ mm. in diameter, and are well preserved.

Specimen T90.—A small, very well-preserved disc specimen, approximately 3½ x 2½ inches in transverse section and about 2¾ inches long. Serial sections were made of this specimen, and the branching of three of the stems was followed for a distance of 4½ cm., as illustrated in text-fig. 4. Approximately 55 stems are found in a single transverse section, of which 22 are in various stages of dichotomizing. Individual stems vary from 1½ to 4 mm. in diameter, with most stems measuring 3 mm. in diameter. Preservation of the stems varies somewhat, although in no apparent set pattern.

Specimen T229.—This is a rather large disc specimen (fig. 9) and is especially unique in that it is crescent-shaped in transverse section, the latter measuring nearly 13 x 6 inches. Two discs, totaling about 12 inches long, were found, one of which is in Mr. Thomas's collection and one in ours under the above number. Most of the stems are in a rather advanced state of decay, due primarily to the fact that the specimen came from toward the lower part of a trunk as is indicated by the fact that many of the stems are invaded by numerous roots.

ASSOCIATED PLANT REMAINS

In his description of *Tempskya wyomingensis* Arnold ('45) has mentioned "occasional fragments of the trunks of *Cycadeoidea*, which resemble those from the Freezeout Mountain locality north of Medicine Bow" associated with the fern material in the valley of Beaver Creek, Bighorn County, Wyoming. Aside from that reference, nothing has been reported so far as we are aware concerning the plants with which *Tempskya* may have been associated in life.

We have been fortunate in finding in section 27 (Lanes Creek quadrangle, see text-fig. 1) rather abundant fragments of a dicotyledonous wood, a coniferous wood, and a portion of the trunk of a *Cycadeoidea*. Although these plant remains were found only in the one locality they serve to give us some concept of the ecology of the Tempskyas.

Judging from the very faintly defined annual rings of the fossil woods seasonal climatic fluctuations probably were not great, and the presence of the cycad, as well as the cycad and dinosaur fragments reported by Arnold, would suggest a generally warm climate. If the growth requirements of *Tempskya* were at all comparable with those of modern tree ferns the climate must have been a tropical one.

In trying to arrive at a tentative comparison with modern floras and climates we have drawn on the extensive field experience of Mr. Paul H. Allen, the Garden's tropical plant collector in Central America. The following is, we feel, of some comparative significance:

> "The only modern conifers associated with tree ferns in the American tropics would be species of *Podocarpus*, usually found in the highlands between 3000 and 7000 feet. Slender

species of tree ferns occur as isolated specimens in heavy rain forest from sea level to 6000 or 7000 feet, being replaced by stouter, handsome species at higher elevations. Greatest concentrations of individuals, however, are found in open, unshaded locations having ample moisture, such as banks of small streams in pastures (vicinity of Villavicencio, Meta, Colombia), abandoned fields growing up to second growth (highlands of Chiriquí—4,000 to 6,000 ft.), moist sunny canyons in dry grassland (badlands of lowland Coclé), or sunny moist roadside banks in forested areas (vicinity of Puerto Pilon, Canal Zone), or National Highway near Remedios, Chiriquí Province, Panama. No true cycads occur in the Americas in close association with tree ferns in modern times, but I have seen species of *Zamia* growing in the same area with them about Madden Lake in the Zone, and in patches of forest along the Rio Ariari in Colombia.

"Summarizing, tree ferns grow in greatest concentration in relatively open, sunny situations, and there is, so far as I know, nothing that could be described as a typical tree-fern association of plants. Thus, while tree ferns might by pure coincidence be found with *Podocarpus* or *Zamia*, they might just as often, or rather more often, be found with other things."[5]

In a consideration of the climate of this region during middle Upper Cretaceous times it is pertinent to recall the presence of *Anemia Fremonti* and *Gleichenites coloradensis* in the Frontier formation of southwestern Wyoming. These are fern species with undoubted relationships to the modern genera *Anemia* and *Gleichenia*, both of which are tropical to warm sub-tropical in their present distribution. Although the fossils were found south of Kemmerer, Wyoming, the Frontier formation extends north to a point less than 25 miles from Wayan, and the actual distance to the Kemmerer locality is less than 100 miles.

We do not know what the exact correlation is between the Frontier and Wayan formations; the latter may lie slightly below the former (Read and Brown, '37, pl. 27). Yet, it is safe to assume that the two are not far apart. Thus since these two ferns of tropical affinities were contemporaneous and inhabited the same area, or very nearly so, as the Wayan *Tempskya* flora, we are inclined to consider this southeastern corner of Idaho and adjoining Wyoming as being clothed in tropical forests covering undulating hills of altitudes up to possibly 4000–7000 feet, and favored by a climate that was uniformly moist and warm throughout the year. The more exact floristics of the "*Tempskya* forests" must remain in doubt, although the Colombia and Canal Zone habitats suggested by Mr. Allen seem to present a very likely comparison.

Tempskya as animal food.—It does not seem entirely improbable that the Tempskyas constituted an important dietary item for certain larger animals of the time, such as the Cretaceous herbivorous dinosaurs. Diversified as the dinosaurs were in form and environmental adaptations, some of them almost certainly must have occupied the habitat of these ferns. The association of their bone fragments (see p. 124) with Tempskyas adds support to this belief.

If our concept of the habit of *Tempskya* is correct it presented an ideal browsing plant. With the foliage distributed over a considerable portion of the trunk, rather than in merely a crown at the top, the leaves were available to herbivores both small and large. Each plant bore a considerable quantity of foliage even though the individual leaves were small. From the abundance and wide distribution of the Tempskyas in certain regions it would seem possible that they may have been of considerable importance as animal food.

[5] From a letter received from Paul H. Allen, Gamboa, Canal Zone, May 7, 1946.

BENNETTITALES

Cycadeoidea sp.—In the summer of 1946 Mr. Thomas found two cycad specimens in section 27 (see text-fig. 1). One of these is a very small fragment while the other, described here briefly, is a portion of what was apparently a columnar trunk and measures 7 inches long and 9 x 7.5 inches in diameter. Its owner has preferred that the specimen remain intact, and since it is rather poorly preserved and with no strobili in evidence it is doubtful whether sectioning would reveal significant evidence. In the transverse section the leaf base zone is about 1.5 inches wide, while the entire central portion of the trunk is largely replaced by silica. At one point a small fragment of the wood is intact and measures slightly less than 2 cm. thick. Like the *Tempskya* specimens, this cycad trunk fragment shows no evidence of prolonged water transport; thus its chief interest lies in the probable association of these plants with the ferns in the Cretaceous landscape of the Wayan region.

CONIFERALES

Cupressinoxylon sp.—In transverse section (fig. 31) this wood presents two conspicuous features: (1), the annual rings are not sharply defined, there being very few "late summer" tracheids marking that year's growth from the first cells of the following year; and (2), resinous parenchyma is profusely scattered through the wood.

In tangential view (fig. 32) the rays may be seen to vary from 2 to 40 cells high and predominantly uniseriate with an occasional biseriate one. There is no evidence of pitting in the tangential walls of the tracheids. The preservation is not sufficiently good to allow observation of the finer diagnostic details in radial section. Tracheidal pitting, however, is of the abietinean type and, for the most, part uniseriate, while the rays appear to be uniformly parenchymatous, there being no evidence of ray tracheids.

DICOTYLEDONEAE*

SOME NOTES ON METHODS

The problems of studying effectively silicified trunks that range up to 16 inches in diameter need hardly be emphasized. Furthermore, although the abundance in which the fossils were found during the second and third trips to Wayan was most encouraging, one could not help but wonder whether a sufficiently comprehensive study could be completed within a reasonable period. In general, we have selected only the more complete and apparently better-preserved speciméns for microscopic study. Some sort of critical concentration of material was obviously necessary at the outset, and while specimens of importance, possibly representing new species of significant morphological features, may have escaped our attention we do not feel that the number is high.

In preparing study material recourse has been made to the ground-section and the peel methods. Specimens up to about 5 inches in diameter were cut in our own laboratory, while the larger ones have been cut by the Pickel Stone Company

* As it has not been possible to prepare a discussion of the associated dicotyledonous wood without seriously delaying publication this will appear at a later date.

of St. Louis. Such firms, having equipment for cutting and polishing large monument stones, may prove of considerable aid in paleobotanical work, and the cost is not excessive.

In all cases we have first made peel preparations of the complete transverse section. There is almost no limit to the area of a section made with this method provided adequate cutting and grinding equipment is available. These peel preparations proved invaluable in studying the gross organization of the trunks as well as detailed cellular anatomy in the better-preserved material. A few other points with reference to the peel technique seem worth recording. The quality of preservation in different portions of a peel taken from a transverse section often varies considerably. Generally, in the larger trunks, the central portion is not as well preserved as the more peripheral parts. This would be expected in accordance with our concept of the mode of growth of the trunks. In some, mineralization apparently was not uniform throughout the trunk.

Especially important is the fact that the degree of etching prior to pouring the peel solution had to be especially precise in this material, far more so than in any other petrifactions that we have studied. As typical of this we may point out the differences observed in the parenchymatous inner cortex of the stems where that tissue is bounded on the inside by sclerotic nests and often on the outside by a thin sclerotic band. With the proper etching time these sclerotic tissues stand out in striking fashion. However, when the time was too long, very dark peel resulted, or when the time was too short, the peels were so light that such tissues could hardly be distinguished at all. In this respect Arnold ('45, pp. 27–28) reports that in *T. Wesselii*, "A peculiarity in the chemical make-up of these stone cells is that in sections prepared by the 'peel' method they are not recognizable, which indicates that they are soluble in the hydrofluoric acid used in the etching process." While this may be true in some specimens it has been our experience that the peels can be made to show the sclerotic tissues just as well as ground sections although some experimenting must be done with the etching time to have it perform to the best advantage.

Ground sections have been prepared from the better-preserved specimens. These have revealed certain of the more minute cellular details, especially in the root structure, in a more satisfactory manner than peels. Most of the best *Tempskya* specimens are black, indicating the presence of a large percentage of the original organic matter. These necessarily must be ground very thin to render sufficient transparency. We have found that the thermoplastic cement known as "Lakeside No. 70," prepared by the Lakeside Chemical Company in Chicago, is far superior to balsam as an adhesive. It is convenient and economical to use, sticks very tenaciously to glass, and does not, as is often the case with balsam, present the difficulty of being too soft or too brittle.

SUMMARY

1. Fossil plants referable to the genus *Tempskya* have been known for over a century from European localities including England, Bohemia, and Russia. More recently a number of species have been described from northwestern United States.

2. The *Tempskya* trunk (false-stem) is composed of many branching siphonostelic stems held together by a dense mass of small, diarch, branching, sclerotic roots. Over 200 stems have been found composing the trunk of some specimens.

3. The specimens described in this report were collected in southeastern Idaho chiefly in the vicinity of Wayan, and have weathered out of the Upper Cretaceous Wayan formation. Other specimens have been obtained from a locality east of Ammon, Idaho.

4. The largest specimen measures 16 inches in diameter although fragments of others suggest a somewhat greater maximum size. It is calculated that a trunk 10 inches in diameter attained a height of approximately 12 feet, while the largest ones may have reached heights of 19 or 20 feet. The trunks were erect or very nearly so.

5. In transverse section the trunks vary from circular to strongly flattened, although in nearly all cases the departure of the petioles indicates radial symmetry. It seems very likely that the flattening has been caused by crushing prior to silicification.

6. In larger trunks the basal portion consists of roots only. As the stems in this region decayed their place was taken by roots.

7. Lateral and longitudinal growth took place by frequent branching of the individual stems, one of the two usually soon ceasing to grow. The leaves were small judging from the relatively minute size of the petioles, although they were very numerous on the trunk as a whole. The leaves were given off in two rows from each stem and probably were borne over two-thirds or more of the length of the trunk instead of only in a crown as in modern tree ferns and cycads.

8. A detailed consideration is given of the organization and apparent physiology of the roots.

9. Comparisons are drawn between certain living species of *Hemitelia* and *Todea* as well as a Carboniferous *Clepsydropsis*. The highly peculiar anatomical organization of *Tempskya* does not compare closely with that of any other fossil or living plant although those mentioned above, among others, seem to present a similar "growth tendency" which apparently originated independently in a number of fern groups.

10. A synopsis (taken from the works of Read and Brown, and Arnold) is given for the better-known American species, and all of the specimens on which this paper is based are referred to *Tempskya Wesselii* Arnold. It seems clear that all of the American species were closely related and very similar in general habit.

11. Spores and sporangial annuli have been found in two specimens.

12. Associated with the *Tempskya* trunks in the Wayan district are fragments of coniferous and dicot woods, and a specimen of a cycadeoid.

ACKNOWLEDGMENTS

I am sure that my friends in Idaho have wondered, during the years that have elapsed, about the little there was to show in the way of published results, and this paper is brought out with a feeling of deep gratitude for their cooperation and patience and the hope that some measure of worth and satisfaction has rewarded their efforts.

For his generosity and ever-ready willingness to guide me along the little-known paths of his state I am very grateful to William A. Peters of Jerome, Idaho. Sincere thanks are also due Ralph and Blanche Peters. A very large share of the credit for whatever contributions may have been made to the story of the Tempskyas is due Henry Thomas, of whom appreciation has been recorded elsewhere in the text. For the specimens obtained from the Ammon locality thanks are due Mr. E. Manion, of Firth. Last but not least it is a pleasure to acknowledge the kind hospitality of the ranchers of Wayan whose cooperation in many ways has added immeasurably to the success of the field work.

We are also indebted to Dr. C. A. Arnold for kindly presenting specimens of *T. Wesselii* and *T. wyomingensis* from his own collections.

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Explanation of Plate

PLATE 15

Fig. 1. A representative view of the hills southeast of Wayan, Idaho. Numerous specimens were found along the slope in the center, and on the left slope of the hill in the background.

Fig. 2. Mr. Henry Thomas and a portion of his *Tempskya* collection. Wayan, Idaho.

1

2

ANDREWS & KERN—IDAHO TEMPSKYAS

Explanation of Plate

PLATE 16

Fig. 3. A specimen of the basal end of a trunk showing roots only; basal circumference of specimen 36 inches, upper circumference 32 inches. This specimen differs from most in that the under side of the base is uniformly hollowed, forming a large single cavity with a maximum depth of about 1 inch in the center. Thomas collection.

Fig. 4. A portion of a trunk showing somewhat more rapid tapering than is usual in one of this length; basal circumference 29 inches, upper circumference 24 inches, length 13 inches. Thomas collection.

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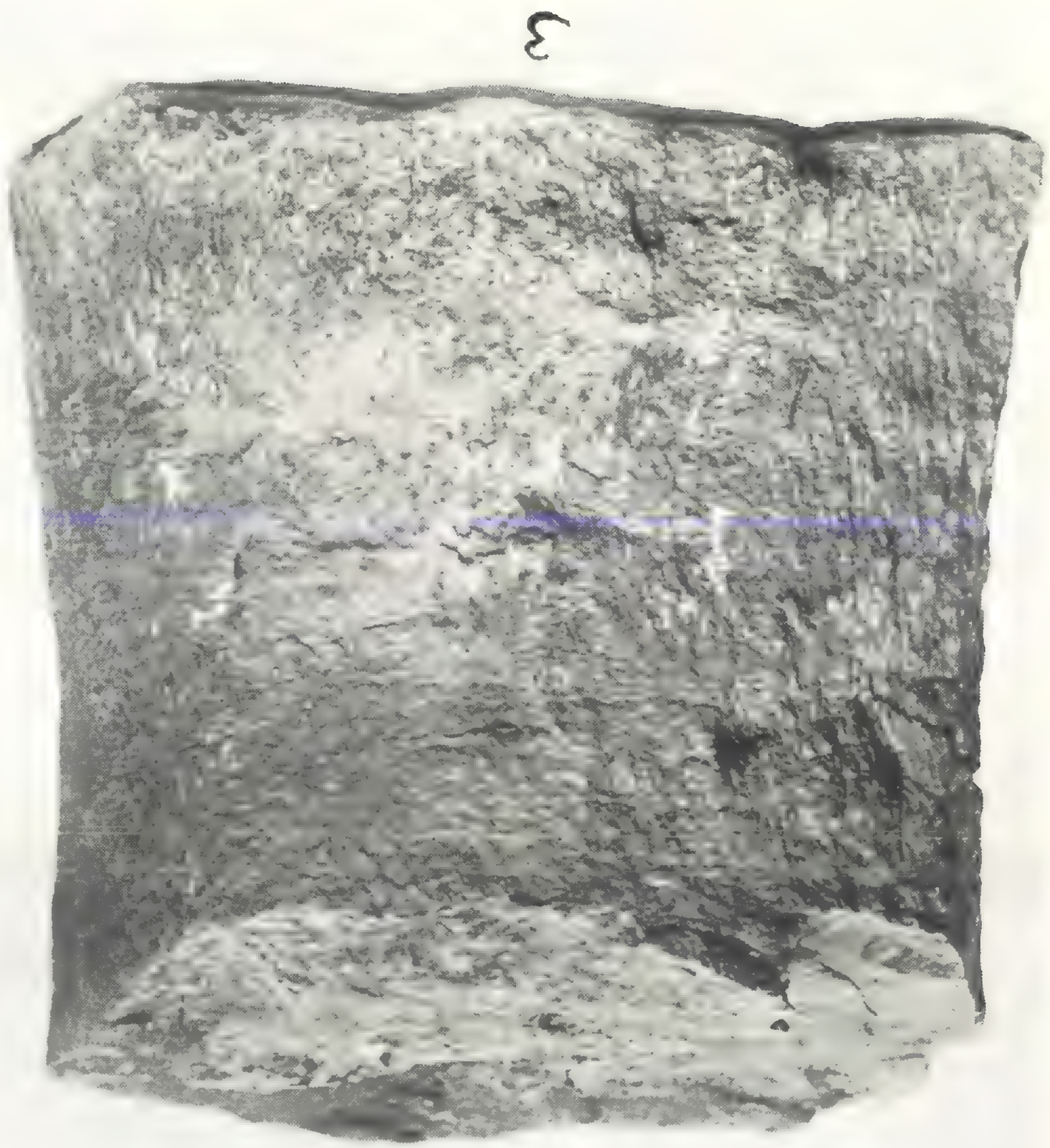


PLATE 16

Explanation of Plate

PLATE 17

Fig. 5. A basal portion of a trunk nearly circular at the bottom and somewhat flattened above.

Fig. 6. A view of the under side of the base of the same. Henry Shaw School of Botany collection, T83.

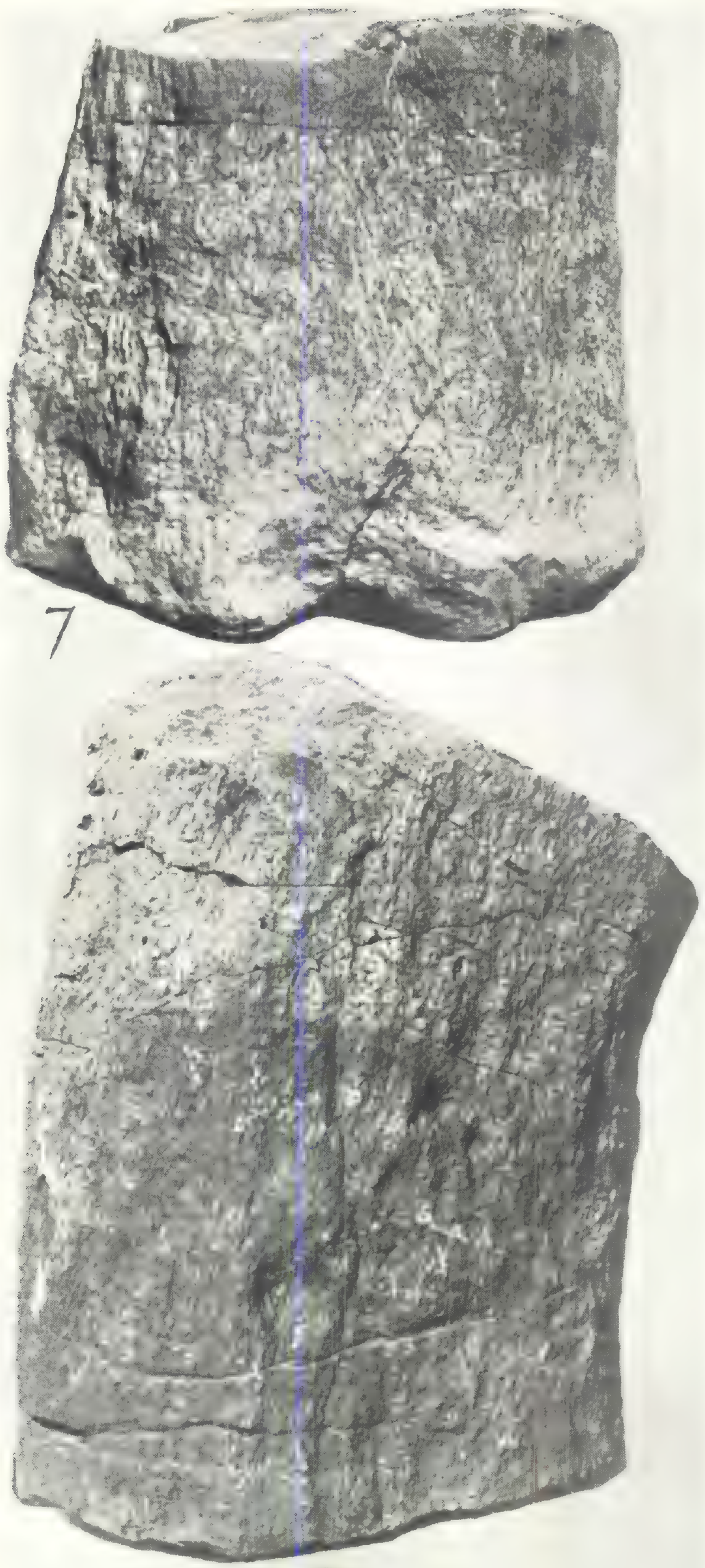
ANDREWS & KERN—IDAHO TEMPSKYAS

EXPLANATION OF PLATE

PLATE 18

Fig. 7. A typical specimen of the base of a trunk, composed only of roots; circumference at upper end 23 inches. Thomas collection.

Fig. 8. One of the two specimens in the entire Wayan collections which shows any appreciable curvature; lower circumference 25 inches, upper circumference 22 inches. In transverse view this specimen is somewhat flattened, the diameters of the upper end being 4¼ x 8¼ inches respectively. Thomas collection.



ANDREWS & KERN—IDAHO TEMPSKYAS

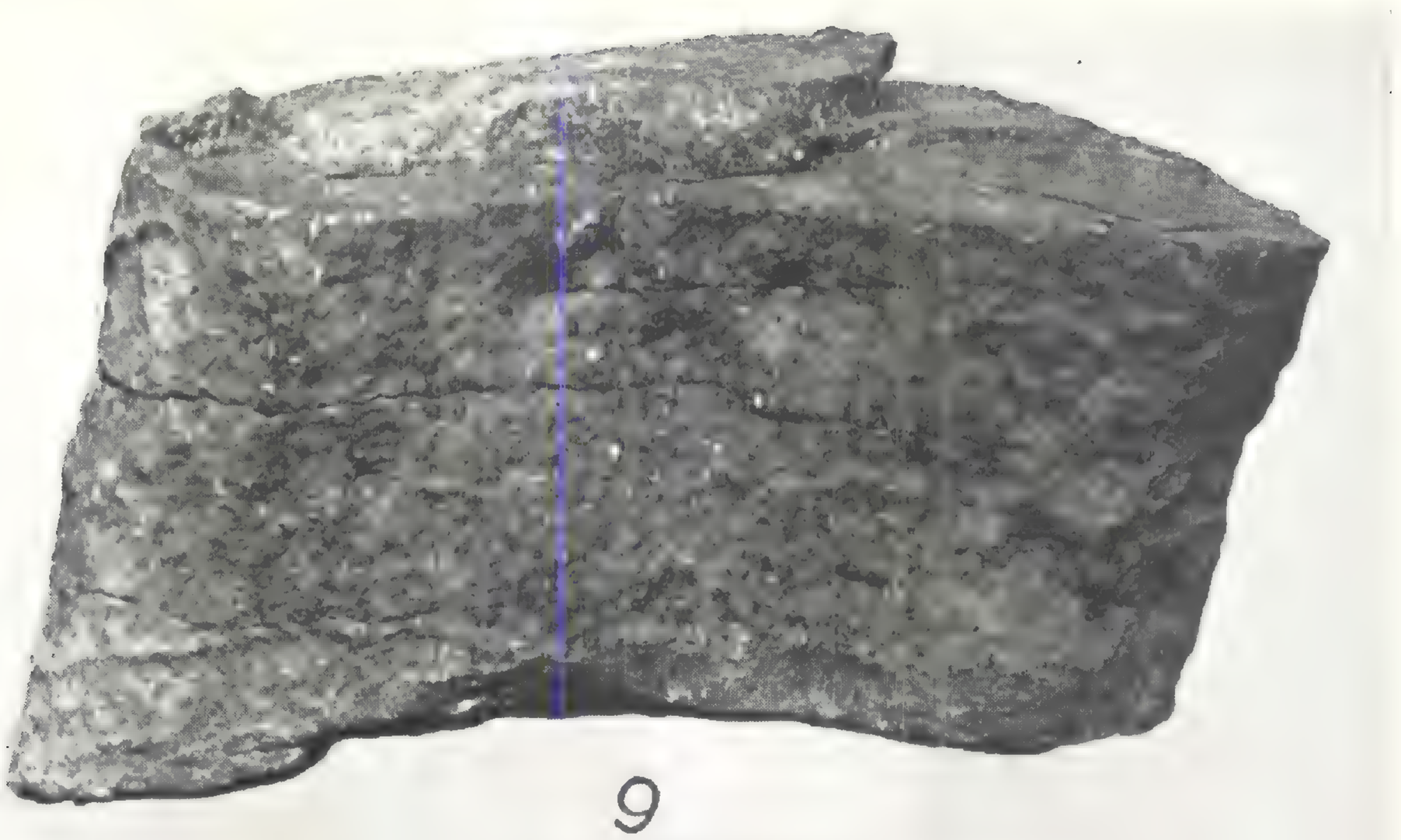
Explanation of Plate

PLATE 19

Trunk (disc) specimens of *Tempskya* showing the flattened form in which many are found.

Fig. 9. A rather large and unique specimen in that it is crescent-shaped in transverse view. This is a short disc, the major and minor diameters measuring 13 x 6.5 inches. Henry Shaw School of Botany collection, T229.

Fig. 10. End view of three disc specimens from the Thomas collection showing varying degrees of flatness in transverse section. The specimen at the left is not a complete disc, the side at the bottom of the photo representing a broken surface. Dimensions of the (transverse) ends shown in the photo are: left, circumference 17 inches, diameters 7 x 2 inches; middle, circumference 17½ inches, diameters 6¾ x 3¼ inches; right, circumference 17 inches, diameters 7 x 3 inches.



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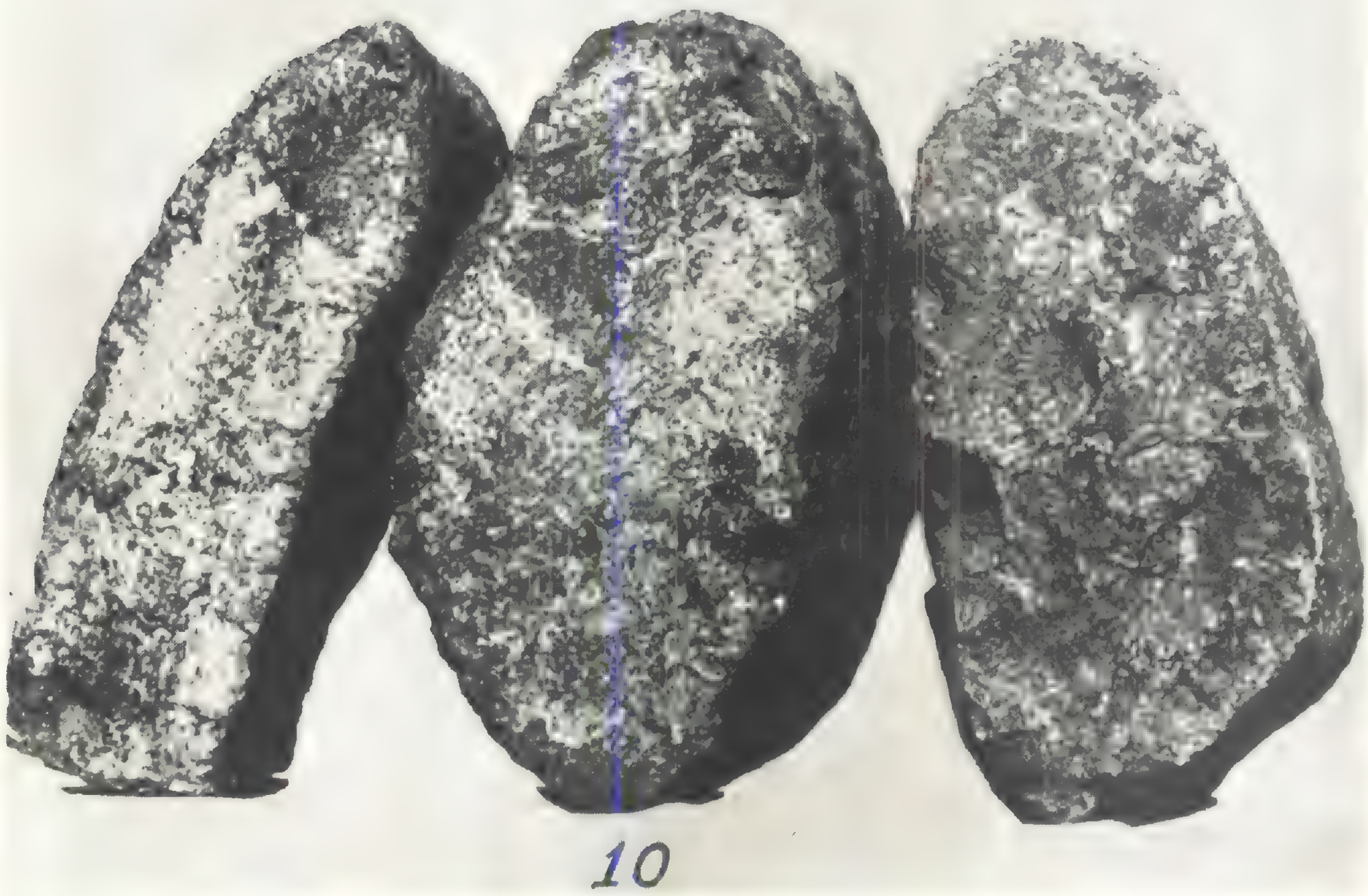

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ANDREWS & KERN—IDAHO TEMPSKYAS

Explanation of Plate

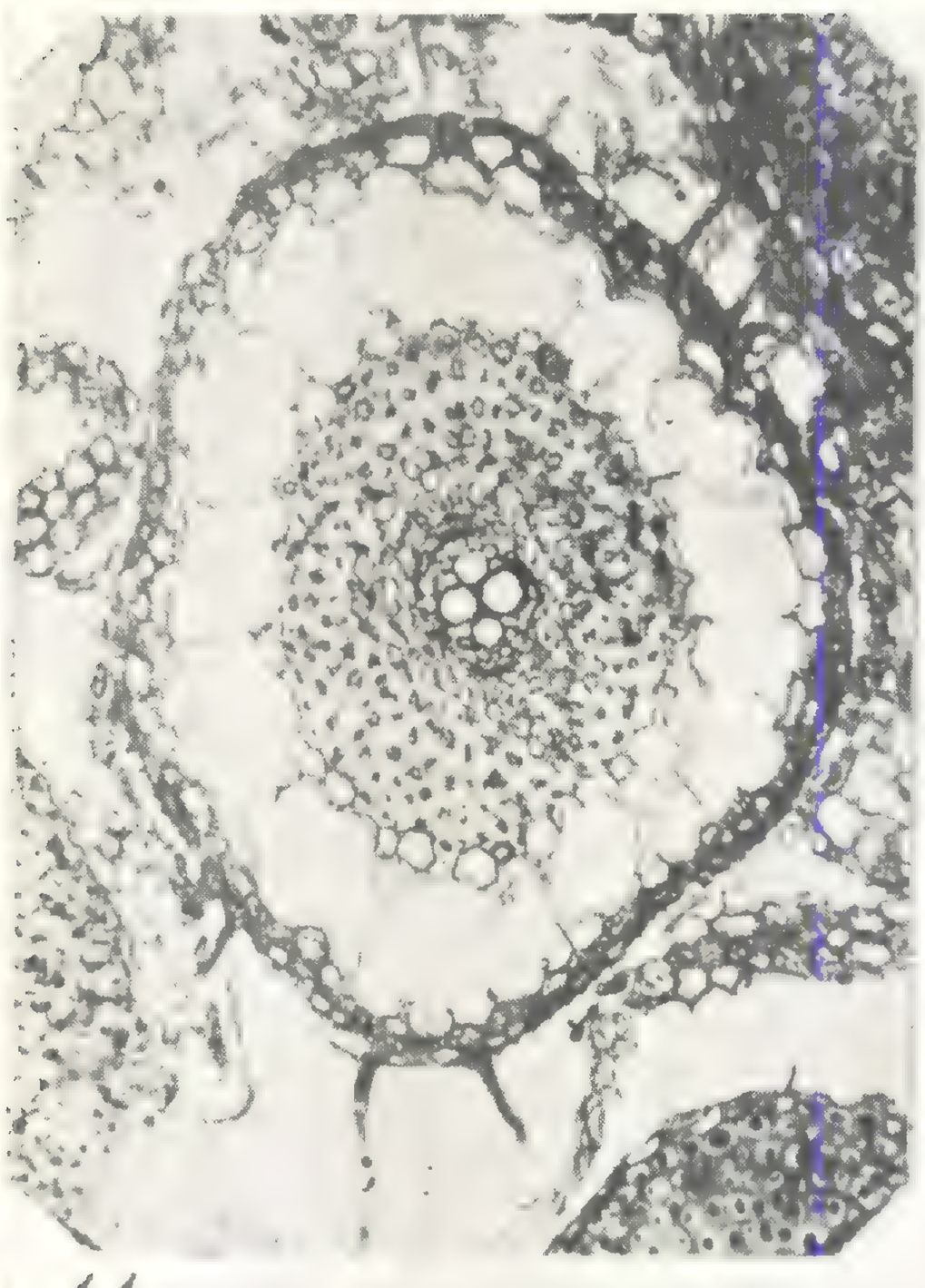
PLATE 20

Fig. 11. An older root showing young root hairs produced on the "loop" of the outer cortex. From slide 1406, x 70.

Fig. 12. Root-hair development of smaller root. From slide 1406, x 80.

Fig. 13. Stelar structure of a root in which xylem, phloem, pericycle and endodermis are distinguishable. From slide 1411, x 175. Detailed description in text.

Fig. 14. A portion of the root mass showing various stages of preservation in adjoining roots, some perfectly preserved, others with merely the circle of sclerotic middle cortex remaining, thus indicating that roots were not all alive but in various stages of decay at the time of fossilization. From peel T53-4, x 17.



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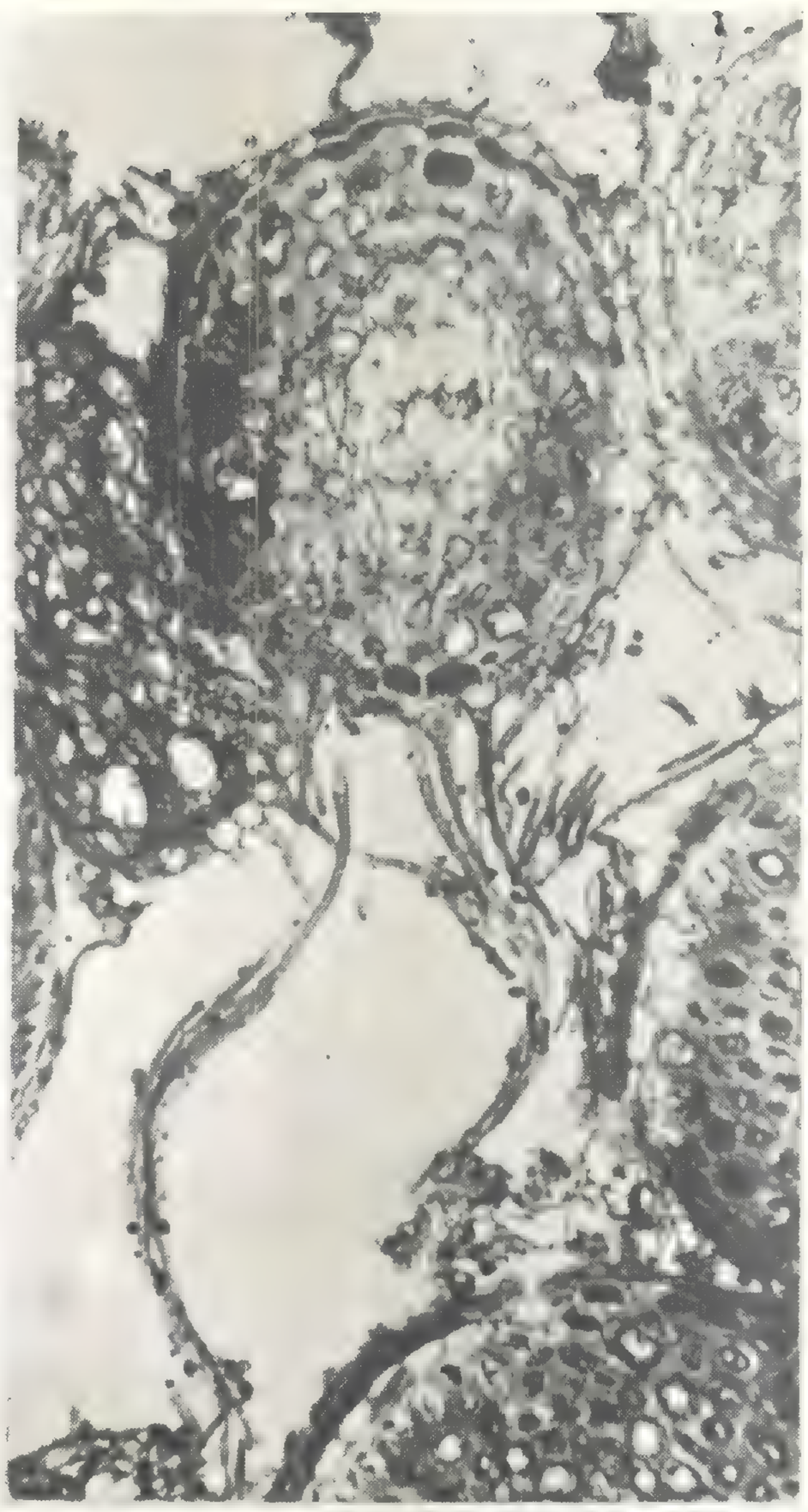

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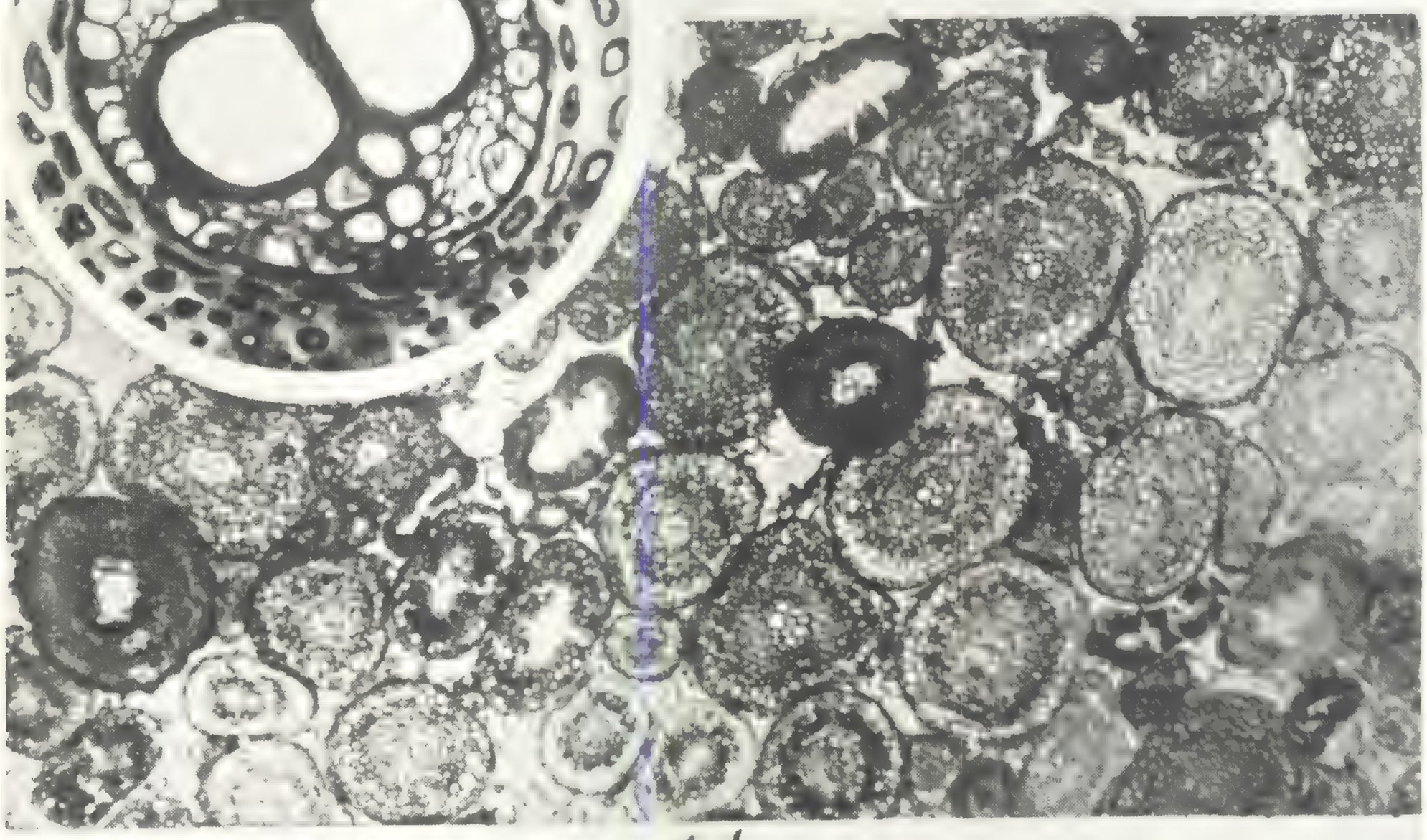

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ANDREWS & KERN—IDAHO TEMPSKYAS

Explanation of Plate

PLATE 21

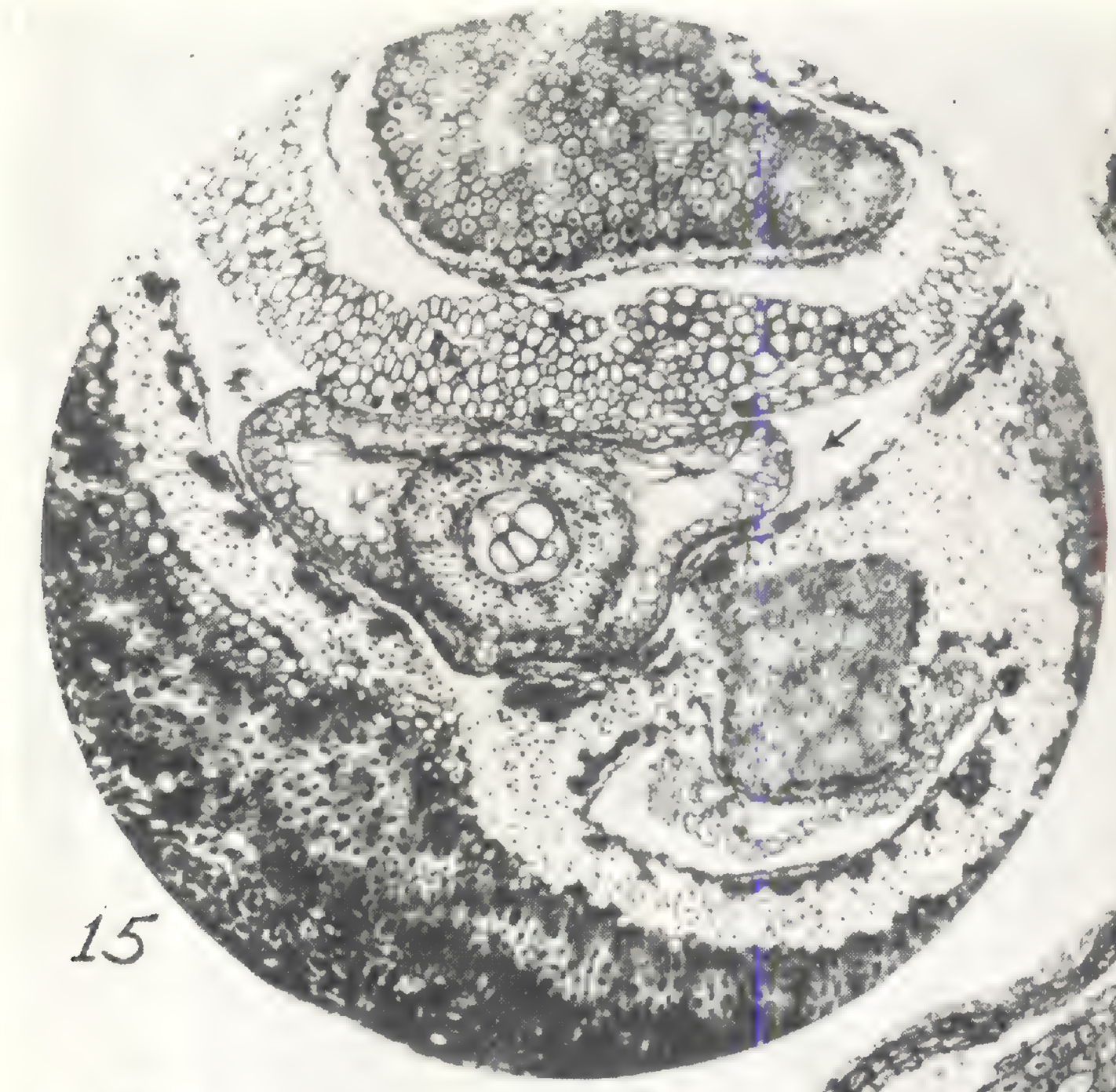
Fig. 15. A small root which has penetrated a stem and is bearing a root hair, indicated by arrow. From slide 1409, x 48.

Fig. 16. Enlarged view of the root hair in fig. 15, x 280.

Fig. 17. A young root with just the beginnings of a sclerotic middle cortex, and the delicate outer cortex complete. From peel T53-2, x 50.

Fig. 18. A very small, but older root, as indicated by the sclerotic middle cortex. From peel T17-11, x 80.

Fig. 19. An older root showing the tangential rows of sclerotic cortical cells and the "loop" produced by the disappearance of the delicate outer cortical cells. From peel T17-8, x 53.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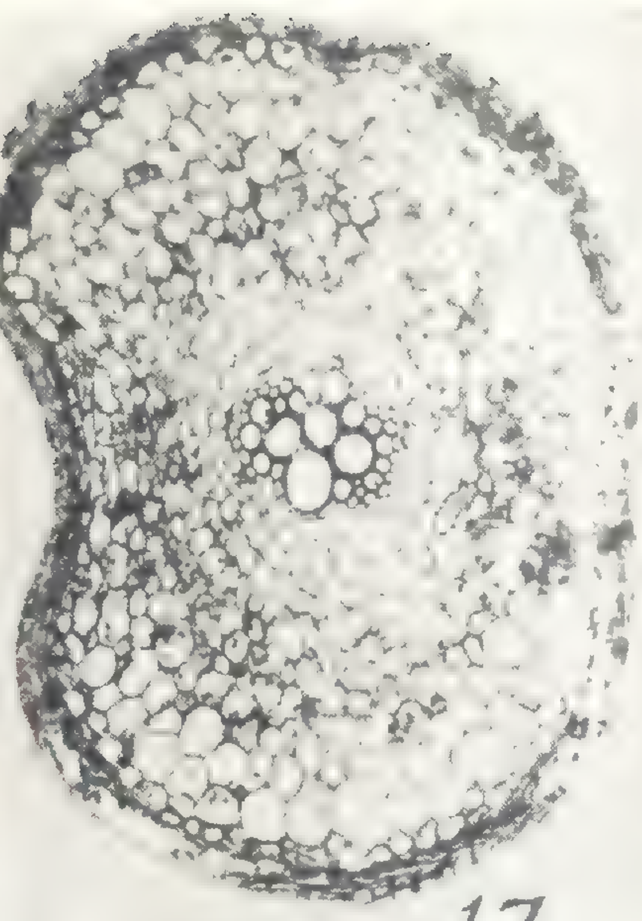
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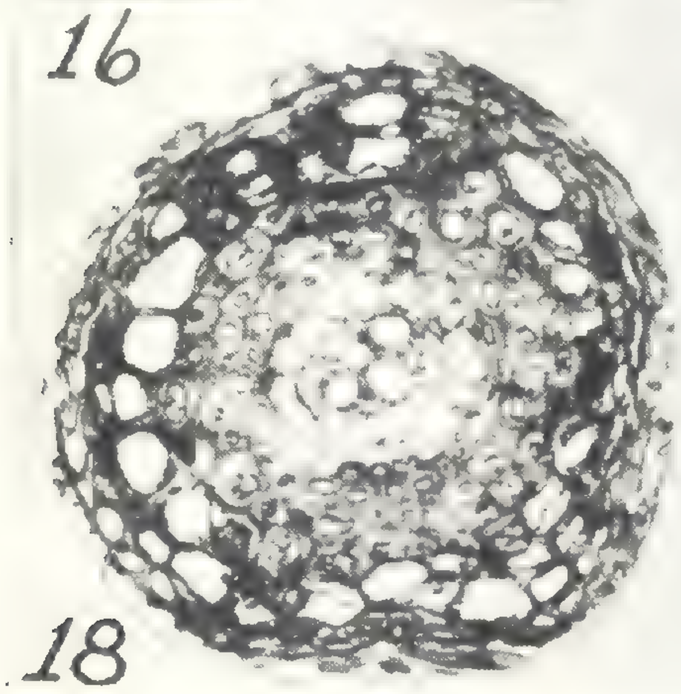
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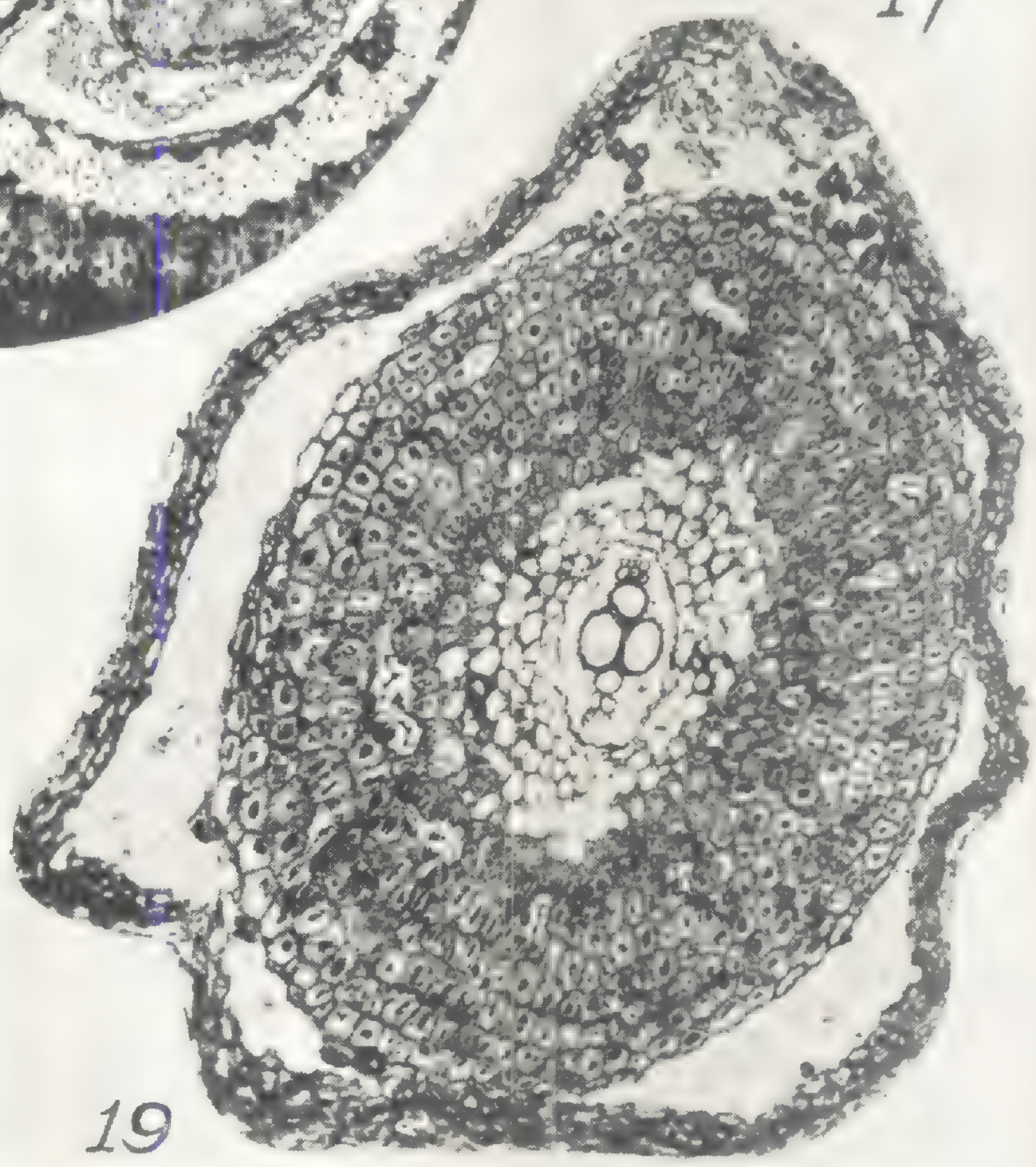
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Explanation of Plate

PLATE 22

Figs. 20 and 21. Two stems found in peel T17-7, illustrating the variation in stelar size in a single trunk section. The large stem shown in fig. 20 bears two leaf traces, *a* and *b*. A third one *(c)* may be seen to be nearly ready to depart from the stem stele. Both figures x 20.

Fig. 22. A stem showing unequal dichotomy, from peel T33-2, x 20.

Fig. 23. One of the spores found down among leaves and stems in specimen T16. From slide 1400, x 500.

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Explanation of Plate

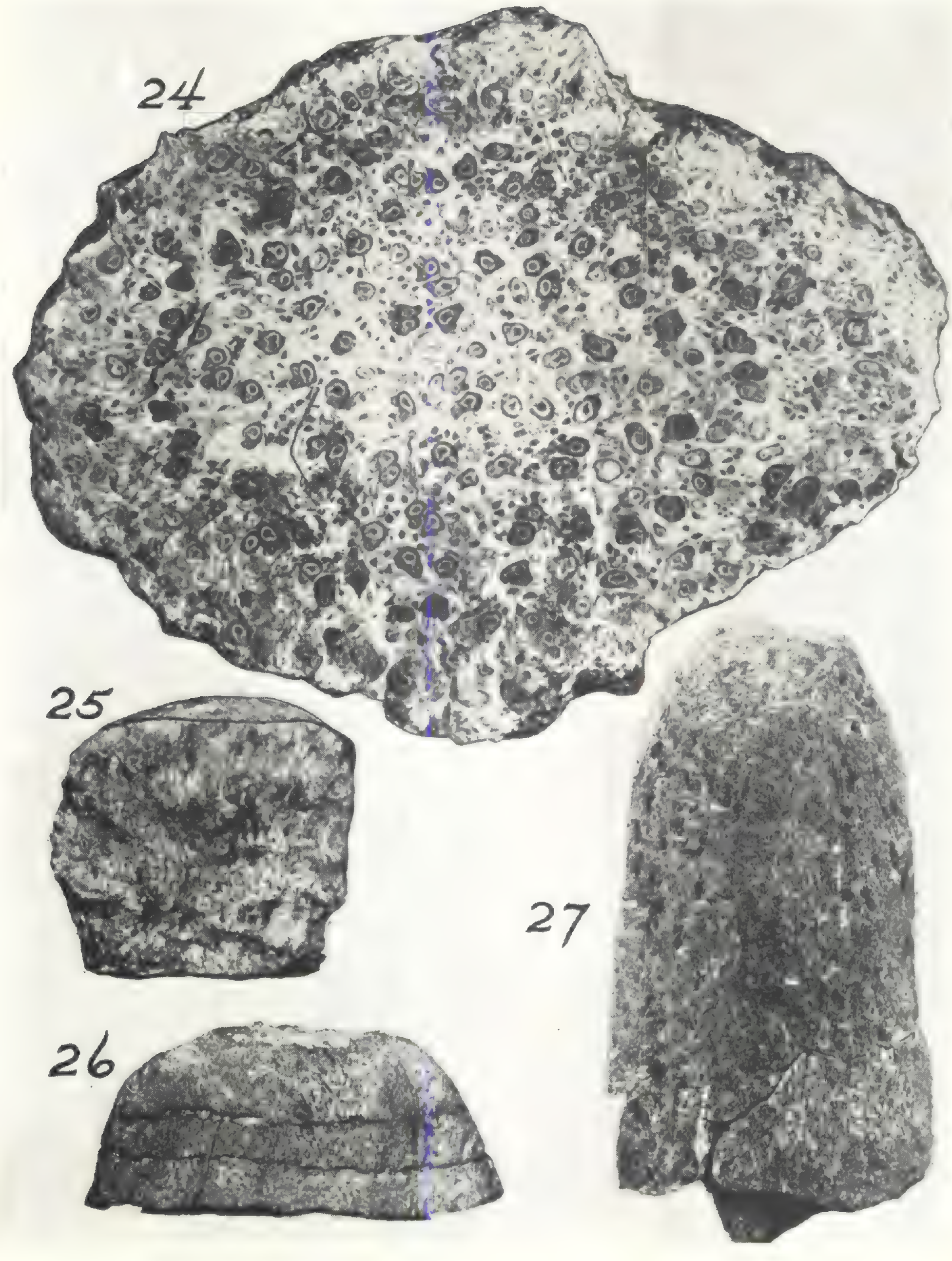
PLATE 23

Fig. 24. A specimen from the Thomas collection, with 192 stems present in its area of 5½ x 4 inches. The specimen was from ⅞ to 1½ inches thick.

Fig. 25. A much flattened disc specimen (T27) which measures 3½ x ⅞ inches in transverse section at the top, and 4½ inches in length.

Fig. 26. A flattened tip specimen (T2) which measures 6½ x 1½ inches in transverse section at the base and 2¾ inches in length.

Fig. 27. A tip specimen (T230) which measures 6 x 3½ inches at the base and 12 inches in length.



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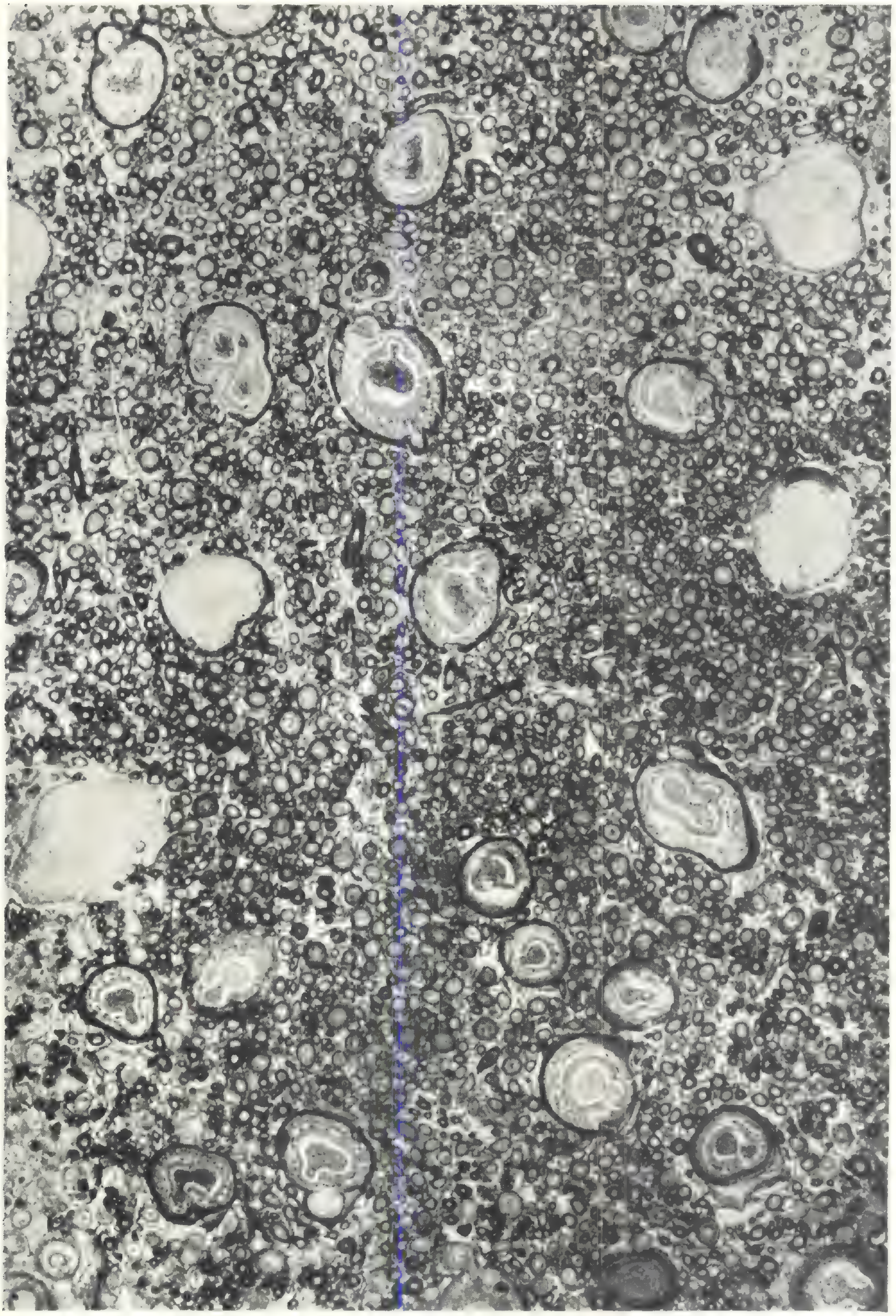
Explanation of Plate

PLATE 24

Fig. 28. Transverse view of part of a *Tempskya* trunk showing about 26 stems. From peel T51, C, T13, x nearly 5.



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ANDREWS & KERN—IDAHO TEMPSKYAS

Explanation of Plate

PLATE 25

Fig. 29. A partially dissected specimen of the modern *Hemitelia crenulata*. From: Schoute, J. C., Eine neue Art der Stammesbildung im Pflanzenreich (*Hemitelia crenulata* Mett.). Ann. Jard. Bot. Buitenzorg, *pl. 10, fig. a.* 1906.

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Explanation of Plate

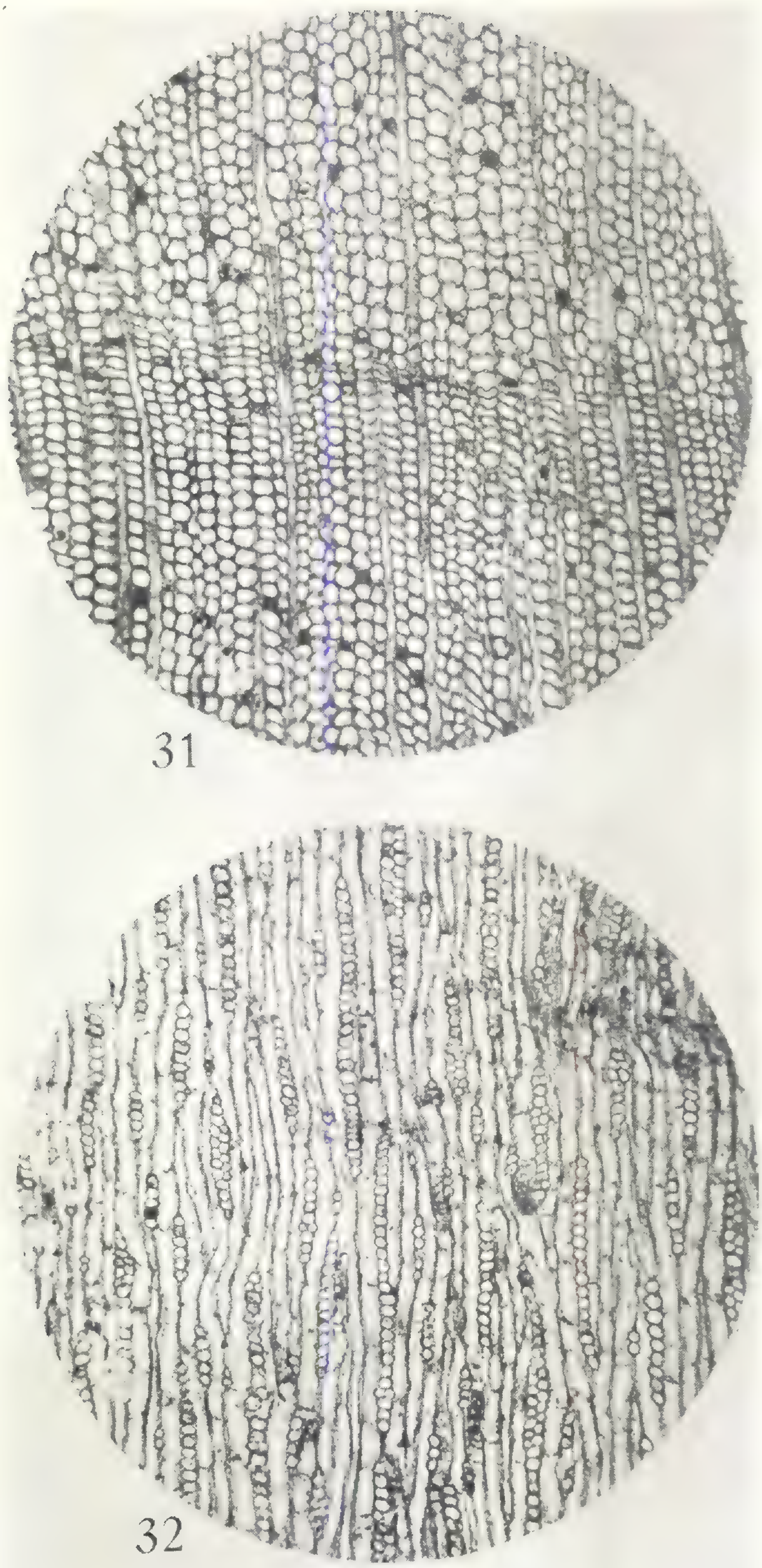
PLATE 26

Fig. 30. A profusely branching specimen of the modern *Hemitelia Smithii* from New Zealand. From: Buchanan, J., On a remarkable branching specimen of *Hemitelia Smithii*. Trans and Proc. N. Z. Inst., *pl. 12*. 1886.

Explanation of Plate

PLATE 27

Figs. 31, 32. Transverse and tangential sections respectively of a specimen of coniferous wood (*Cupressinoxylon* sp.) found associated with *Tempskya* east of Wayan, Idaho. Fig. 31 from slide No. 1474, specimen T8, x 62; fig. 32 from slide No. 1475, specimen T8, x 62.



ANDREWS & KERN—IDAHO TEMPSKYAS

Appendix

SOME COMMENTS ON THE DISCOVERY OF TEMPSKYA IN THE VICINITY OF WAYAN, IDAHO

By C. HENRY THOMAS

In answer to your request I have included in the following lines a brief historical sketch of my *Tempskya*-collecting activities in the Wayan district.

I located in that part of the state in May, 1915, having migrated from the Scottsbluff country in Nebraska where I was raised on the frontier. Mine has been pretty much of an outdoor life. I was born in a one-room sod house in a still untamed country and have herded sheep or otherwise worked with livestock ever since the age of seven. As a boy I roughed and toughed it on the wind-swept prairies of western Nebraska, which were then treeless and monotonous with not even a shrub in sight. But since then they have been put under irrigation and become most productive and desirable.

After locating in the Grays Lake country of Caribou County I became occupied as a sheep herder and was naturally attracted to the odd and out-of-the-ordinary petrified fossil remains which are frequently seen on the range. At the time I did not know whether they were plant or bone, or in fact what they were; it was evident only that they were fossil remains. If bone it seemed most likely that they were saurians, or lizard-like reptile remains, and if plants, I had no idea of their origin.

Most of us are born with a sense of curiosity. We like to pry into the unknown. There are charms in new ventures, and thrills in first discoveries. Moreover, most of us are pack rats. We like to accumulate, although not many become enthralled with rocks.

I started gathering specimens in a small way almost simultaneously with my arrival on the Williamsburg bench. Later, as my collection had grown to a sizeable extent this matter became noised abroad, bringing a number of mineral collectors and rock-hounds from far and near. But no one knew what they were.

Myths and tales precede scientific knowledge. The human mind wants an explanation. And such settings gave birth to wild and fantastic tales. In one instance a certain oil-stock promoter, on visiting Mr. Sam Sibbett's ranch, claimed to be able to trace the outline of some huge bird which was of such gigantic proportions that it could seize an elephant by the nape of its neck! Such were the earlier local concepts of these interesting fossils that we later learned were petrified Tree fern trunks.

In the fall of 1936 I read in the Pathfinder of Mr. Roland W. Brown being associated with the Smithsonian Institution and doing paleontological work in Idaho and other far western states, so I sent some specimens to him for identification. Mr. Brown informed me that they were the so-called Tempskyas, or the petrified remains of a peculiar fern of the Cretaceous period.

Mr. Brown contacted Mr. W. W. Rubey (also of the U. S. Geological Survey) and as a consequence Mr. Rubey, who was doing field work on the Wyoming side

during the summer of 1937, came over to investigate. He expressed surprise at the abundance of Tempskyas in this region, and also took a number of leaf imprints of semi-tropical plants found in sedimentary rocks adjacent to grounds where Tempskyas weather out.

In August, 1938, Mr. Brown and Mr. Carl Mumm came to study the Tempskyas and the stratification of the beds out of which they weather.

Mr. W. A. Peters of Jerome, Idaho, who, of all rock-hounds, undoubtedly has the largest and most diversified collection in the state of Idaho, paid a visit in the spring of 1942 and brought with him Mr. Henry N. Andrews of the Missouri Botanical Garden, St. Louis. Mr. Andrews came at a favorable time of the year, when the snow was gone and there wasn't much vegetation to hide rocks, and the ground was soft so that they could readily be pried out with a wrecking bar. Paleobotanists know best how to appreciate plant remains of past geological ages. All those who have visited here have appeared to be highly interested and have commented on the excellent state of preservation of our Tempskyas.

During the summer of 1943 I herded sheep for Mr. Emil Stoor on ground adjoining my former holdings to the north and east, and that is when I really found most of my larger and better specimens.

This is an ever-changing world. Fossils are the evidence of the existence of former forms of plant and animal life. Scientists by tracing these clues endeavor to read the history of the earth's past geological transformations. Nothing just happens. Everything is the result of preceding forces. A rock is the product of nature's workings in the past.

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MONOGRAPH OF THE NORTH AMERICAN SPECIES OF CORYDALIS[1]

GERALD BRUCE OWNBEY[2]

Introduction

My attention was attracted to the genus *Corydalis* of the family Fumariaceae some years ago, since it seemed to offer many unsolved problems in the systematic interpretation of various species. The genus had received no special attention from any American botanist since the time of Engelmann and Gray, and the proposal of nearly forty new names for members of the genus in America by Fedde during the early years of the present century had made it imperative that their proper status be determined so that scientific literature no longer would be encumbered with superfluous nomenclatorial terms.

A great volume of herbarium material has been available, in the study of which I have attempted to make full use of classical methods. In addition, it was felt that field studies would help in the understanding of some of the more difficult species. With this in view a six-weeks field trip was made through the western United States during the summer of 1946.

I have attempted to view all species in the light of modern concepts of speciation. Population studies of one species have confirmed the presence of minor measurable differences between inbreeding colonies of this species, even those not widely separated geographically. I also have had opportunity to grow several species under greenhouse conditions and to test the stability of minor variants. Further work along these lines doubtless would do much in clearing up obscure problems not amenable to standard methods of the herbarium taxonomist.

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[1] An investigation carried out at the Missouri Botanical Garden and submitted as a thesis in partial fulfillment of the degree of doctor of philosophy in the Henry Shaw School of Botany of Washington University.

[2] Instructor in Botany, University of Minnesota, Minneapolis.

Issued October 31, 1947.

HISTORY OF THE GENUS

Linnaeus[1] included all of the species of fumariaceous plants known to him in the single polymorphous genus *Fumaria*. The subsequent subdivision of this heterogeneous group of plants was left to later authors who attempted to revive names of pre-Linnaean botanists in something resembling their original sense.

The nomenclatorial complications of the generic name *Corydalis* have been investigated by Sprague[2], from whose account the following discussion largely is abstracted. The name has been used in two distinct senses as follows:

(1) *Corydalis* [Knaut, Meth. Pl. 153. 1716; Dill. Cat. Pl. App. 129. *t. 7.* 1719]; Medik. Phil. Bot. **1**:96. 1789. This is *Cisticapnos* Adans. Fam. Fl. **2**:431. 1763 (*Cysticapnos* Gaertn. Fruct. Sem. Pl. **2**:161. *t. 115.* 1791), and is based upon *Fumaria vesicaria* L. This monotypic genus sometimes is united with *Corydalis* Vent., but in the opinion of students of the family, such as Hutchinson and Fedde, it should be retained separately. As the fruit of *Cysticapnos* is inflated and bladder-like, it seems probable that sufficient grounds exist for segregating the species generically from *Corydalis*.

(2) *Corydalis* Vent. Choix de Pl. *t. 19.* 1803. [*Capnoides* Tourn. Inst. Rei Herb. 423. *t. 237.* 1719]; *Capnoides* Adans. Fam. Pl. **2**:431. 1763. Ventenat treated only a single species, *Corydalis fungosa* (*Adlumia fungosa* Greene), which is now universally recognized as a separate genus. The generic name, however, must be credited to Ventenat, even though the single species is referable to *Adlumia*, since the author states in a footnote that his generic concept is founded upon that of Tournefort, who described and figured *Corydalis sempervirens* (as *Capnoides sempervirens*).

Because of the widespread acceptance of the name *Corydalis* in its modern sense, perhaps occasioned by its adoption by de Candolle in his monumental works[3, 4], the International Botanical Congress of Vienna conserved it over *Capnoides* Adans., *Cisticapnos* Adans., *Neckeria* Scop., and *Pseudofumaria* Medik. The conservation of *Corydalis* has insured its permanent use, and has precluded the revival of any other generic name which otherwise might supersede it.

GENERAL MORPHOLOGY

The aerial parts of *Corydalis* are succulent, and annual or biennial in all of our species. The glaucous foliage and finely dissected leaves give a characteristic aspect to the plants.

In distinguishing sections and species, greatest importance is attached to the morphology of the outer petals, stigma, fruits, seeds, and underground parts. An account of the peculiarities of structure and the special terms used in referring to them is given, therefore, in the following discussion.

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[1] Linnaeus, Sp. Pl. **2**:700. 1753.
[2] Sprague, in Kew Bull. Misc. Inf. **1928**:351. 1928.
[3] DeCandolle, Reg. Veg. Syst. Nat. **2**:113. 1821.
[4] DeCandolle, Prod. Syst. Nat. **1**:126. 1824.

Root: The nature of the root is an important diagnostic character in delimiting sections. In annual, winter annual, and biennial species of Section EUCORYDALIS, an ordinary tap root is present. This often is quite succulent and may be somewhat lignified when the plant reaches maturity. The roots of the perennial species must also be classified as tap roots, although they become fleshy at a very early seedling stage. In *C. pauciflora* of Section PES-GALLINACEUS the mature root is tuberous and ordinarily bifurcate. In Section RAMOSO-SIBIRICAE, the seedlings develop a tuberous swelling the first year. This grows to large proportions during succeeding years and often is crushed and flattened by pressure of the soil.

Stem: A rhizome is present only in perennial species of Section RAMOSO-SIBIRICAE. This gives rise apically to the annual stems.

The hollow, annual stems are succulent in all of our species, although sometimes semi-ligneous at the base. They are monopodial in growth except in Section EUCORYDALIS where they predominately are sympodial. The nodes are somewhat abbreviated toward the base.

Leaves: In our species of Section RAMOSO-SIBIRICAE only a single leaf is produced annually until the plants reach flowering age. The number produced in Section PES-GALLINACEUS is unknown, but presumably is low. In all members of Section EUCORYDALIS a basal rosette of leaves is developed prior to the development of the flowering stems. Leaves are produced alternately, the later ones often being progressively reduced in size and intergrading imperceptibly into the floral bracts. The larger stem leaves are petiolate and pinnate except in *C. pauciflora* where they are simple and ternately divided. The primary segments are themselves once or twice pinnatifid or incised. The petioles are somewhat expanded at the base, especially those of the larger cauline leaves. A few sheath-like cataphylls sometimes are present at the base of the stem.

Inflorescence: The inflorescence is a terminal raceme or panicle, the flowers being crowded at first but becoming more distant during and after anthesis through elongation of the floral axis. The floral bracts offer very little in the way of diagnostic characters. For the most part they are successively smaller from the base to the apex of the floral axis. The uppermost are often extremely minute.

Flowers: Corydalis flowers are bilaterally symmetrical. They are dimerous, having two inconspicuous sepals, two laterally placed outer petals, one of which is spurred, and two inner, dorsi-ventrally placed petals opposite the sepals. There is some cohesion but no true fusion of the petal margins at the base. The stamens are arranged in two phalanges of three each, which are opposite the outer, lateral petals. Morphology of all the parts presumably is conditioned to some extent by compression in the bud. Floral structure is quite uniform throughout the genus.

The very much reduced, rudimentary sepals are scarious and fugacious, and function as protective organs only in the early bud stage. Although they are of little diagnostic value, they are described in detail for each species treated in this paper.

The presence of a single spurred petal and the polyspermous fruit are paramount characters in distinguishing the genus *Corydalis* from closely allied genera. The relative size and shape of the spur vary in different species. In measuring the length for this study the distance from the point of attachment of the pedicel to the tip of the spur is taken. The free end of the petal is carinate. This carina is referred to in the following descriptions as the *hood*. It is often provided with a medial exterior fold, the *crest*, and an expanded border of greater or lesser width, the *wing margin*.

The unspurred outer petal is similar to the spurred one with respect to the hood, crest and wing margin. When the flowers are fully developed, the petal sometimes is geniculate immediately posterior to the hood. In Section Ramoso-sibiricae there is a distinct basal gibbosity which probably represents a rudimentary spur.

The two asymmetric inner petals are connate at their apices and enclose the anthers and stigma at anthesis. They consist of an outer broader portion, the *blade*, and a narrower basal portion, the *claw*. Medially, on the outer surface, there is a longitudinal fold which lies between the margins of the outer petals in the bud. In addition, on the exterior basal half of the blade adjacent to the spurred petal, there is another simple longitudinal fold or fleshy protuberance. Morphology of the inner petals ordinarily is not of diagnostic importance below the sectional level.

Each *stamen phalange* consists of three stamens whose filaments are united laterally. The anther of the central stamen is dithecal; those of the outer stamens are monothecal. The phalange opposite the spurred petal is provided with a nectiferous *stamen spur* which extends into the petal spur and is adnate to it for the greater portion of its length. No morphological characters of value in distinguishing species are to be found in the androecium.

Both the stigma and style are persistent. The style is slender, short, and not distinctive in character. The flattened stigma, however, often is quite characteristic. Stigmatic surfaces are located on papillary projections numbering from four to eight in our species. As the projections are somewhat delicate, an unopened flower or large bud should be selected for examination. In these, germinating pollen does not obscure details of structure as it does in older flowers. The nature of the stigma is of considerable diagnostic value, especially in defining sectional lines.

Teratological flowers of the type termed "peloric" have been reported from time to time. I myself have observed two instances of this phenomenon in which both outer petals were spurred.

Cleistogamy in *Corydalis* has been recognized for many years. In *C. micrantha* and *C. pseudomicrantha* the potentiality for cleistogamy is present at all times. In other species it is rare, non-existent, or unrecognized. The problem of self-fertility is well worth investigation. The flowers of all species studied show evidence of germination of the pollen which is clustered around the stigma. Under

such conditions it is difficult to determine just how much self-pollination actually is occurring. Opportunity for cross-pollination is not lacking as witnessed by the large number of insects, both as to individuals and species, that visit *Corydalis* having brightly colored flowers.

Fruit: The young fruit is enclosed by the stamen phalanges at anthesis, and is oriented so that the placentae are opposite the inner petals in the dorsiventral plane and the flattened stigma in the transverse plane. When mature, it is a few- to many-seeded, bicarpellate capsule varying in shape from narrowly linear to broadly elliptical, oblongoid or obovoid, and sometimes flattened at the base. Dehiscence is accomplished by separation of the two valvate portions from the two placentae. In Section RAMOSO-SIBIRICAE the valves roll up elastically from the base and the seeds are scattered to a considerable distance from the parent plant.

All American species of the genus fall into two well-defined groups with respect to disposition of the fruit on the pedicel. In Sections RAMOSO-SIBIRICAE and PES-GALLINACEUS the body of the fruit is geniculate at the base and is reflexed to a marked degree upon erect or spreading pedicels. In Section EUCORYDALIS the fruit is not geniculate and is not reflexed except by actual curvature of the pedicel.

The ovules are campylotropous. At a very early stage a comb-like or sheathing caruncle appears near the point of attachment of the funicle. At maturity the caruncle covers a greater or lesser portion of the seed. The testa is seen to be essentially smooth to variously reticulate or muricately decorated when viewed under magnification. The nature of these decorations, as well as gross size of the mature seed, is of importance in specific diagnosis.

A pathological condition in which the fruits become swollen, spongy and sterile is not uncommon in *C. Caseana* and *C. aurea.* Upon examination such abnormal fruits are found to contain an insect larva. The egg of the adult insect apparently is lodged in the young fruit at flowering time; the resultant larva passes through the early stages of its existence enclosed within the tissues of its host. Faulty interpretation of the peculiar fruit developed under these conditions has led to some confusion in terminology.

GENERIC RELATIONSHIPS

It is not within the scope of this paper to discuss the relative merits of the many genera of the family Fumariaceae. Hutchinson[5] lists eighteen genera from Europe, Asia, Africa and North America, and Fedde[6] proposes one additional genus from Asia. In North America only four genera are represented, namely, *Fumaria, Dicentra, Adlumia,* and *Corydalis.* All of our species of *Fumaria* are weeds introduced from Europe.

The genus *Corydalis,* the largest of the family, includes a heterogeneous aggregate of species all of which, however, have certain fundamental characters in common. The petals are free or essentially so, and the corolla is zygomorphic,

[5] Hutchinson, in Kew Bull. Misc. Inf. **1921**:97. 1921.
[6] Fedde, in Engler & Prantl, Nat. Pflanzenf. ed. 2. **17b**:121. 1936.

having a single spurred petal. These two characters distinguish the genus clearly from *Adlumia*, which has petals united below, both of the outer ones barely saccate at the base, and, furthermore, it is of climbing habit. The genus *Dicentra* has both outer petals equally spurred, but does not differ fundamentally in any other respect from *Corydalis*. The fruit of *Corydalis* is a 2- to many-seeded, dehiscent, bivalvate capsule, while *Fumaria* has an indehiscent, one-seeded fruit.

The distinctions between extra-American genera of the Fumariaceae and *Corydalis* are of like magnitude to those of the American genera. An important element in the family is its naturalness and the equal systematic value of the features characteristic of its included genera.

Evolutionary Tendencies and Interspecific Relationships

A discussion of evolutionary tendencies often is speculative. The initial assumption generally made is that distant or close genetic relationships are indicated

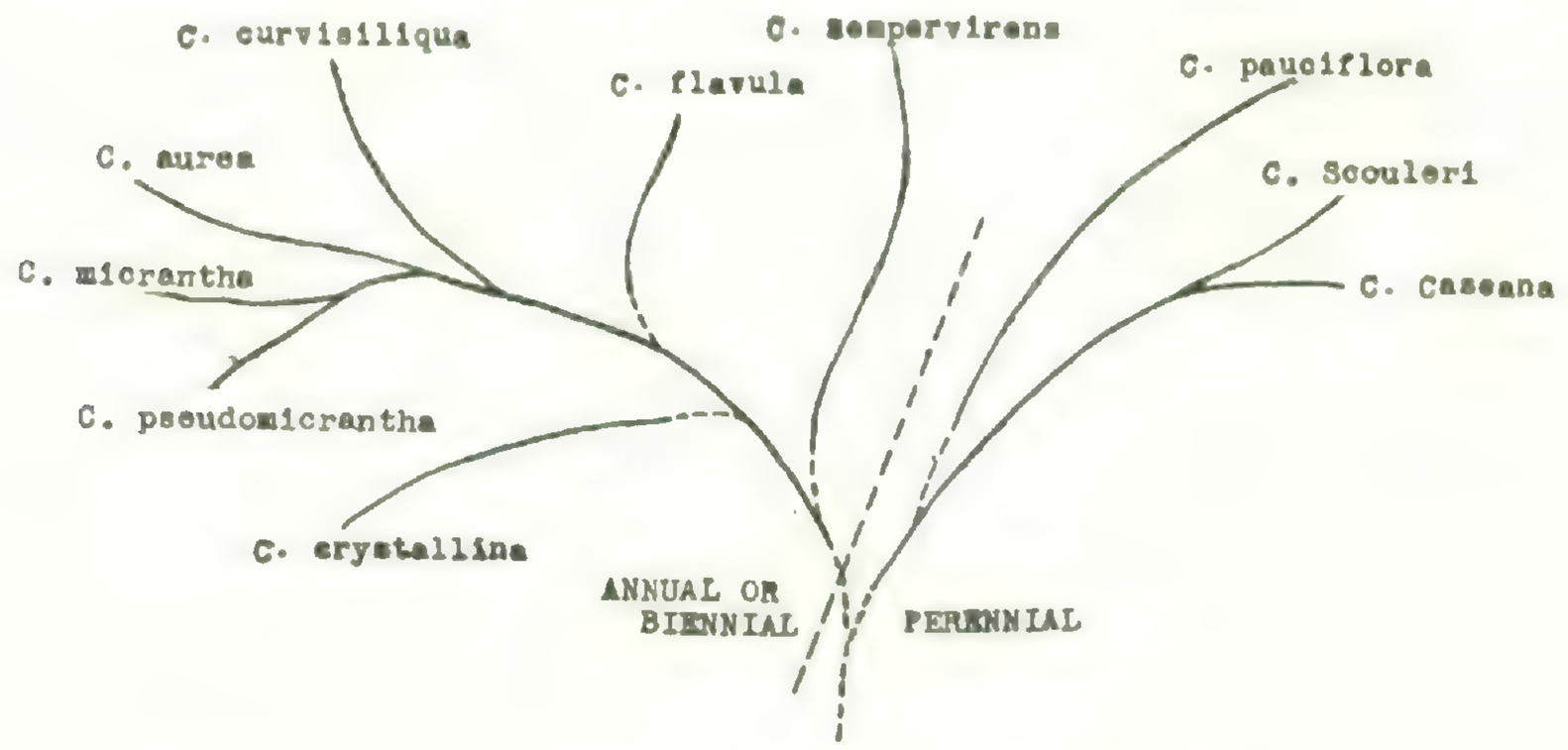


Fig. 1. Suggested interspecific relationships.

by greater or lesser morphological similarities. This assumption ordinarily is justifiable providing due consideration is given to such modifying factors as parallel evolution. Discussions of this nature also are of value in bringing into perspective the probable direction of evolution within the group, and serve to emphasize not only inter-relationships of species, but the characters which are undergoing basic change. This makes possible a prediction of the type of subsequent change to be expected.

Annual species usually are assumed to have arisen from perennial species by compression of the life cycle into a single year. Many genera have both perennial and annual species, *Corydalis* being such a genus. Presumably, one or more lines of perennial species have given rise to the annuals which now predominate in America.

Among perennial species of *Corydalis* are some with rhizomes and some with tuberous roots, one of which type may have given rise to the other at some time in the past. Also, among perennials are species with pinnate leaves and those with sim-

ple, ternately divided leaves. The upper stem leaves of the pinnate-leaved species are much reduced, and, strictly speaking, are simple. Historically, a species with simple leaves could then be derived from one with compound leaves by a foreshortening of the axis or by a reduction of compound leaves to their terminal segments. It is not improbable that this has occurred in *Corydalis*.

Among both perennial and annual species are those with paniculate and those with racemose inflorescences. The racemose type could be derived from a paniculate type by reduction of branching.

In some annual species, such as *C. aurea*, both sympodial and monopodial growth is found. Racemes in both types are terminal. After flowering of the primary raceme in the sympodial type, growth in length is taken over by the uppermost axillary shoot. This in turn gives rise to a terminal raceme. The evolutionary significance of the sympode is not clear. I believe, however, that it should be looked upon as derived from the monopodial type. It may represent only an adaptation for continued growth provided conditions remain favorable.

Concept of Species and Subspecies

I have attempted to portray the species as natural, biological units, the members of which are more closely related genetically to one another than to members of other species. Closeness of genetic relationship is manifested by relatively close morphological similarities. Comparative morphology, then, remains the most immediately usable criterion of genetic relationship. The individuals of each species are potentially interfertile, or at least their historical progenitors were interfertile. Further, each species occupies a "natural" distribution determined by factors inherent within it.

Great morphological variability in some species of *Corydalis* makes over-all statements of distinguishing characteristics of species and subspecies misleading if unqualified. There apparently is a corresponding amount of genetic diversity in some of these plastic or polymorphic species. *C. aurea*, for example, is relatively uniform throughout the northern part of its range. In southwestern United States it breaks up into innumerable forms or ecotypes. According to recent concepts, these may be looked upon as expressions of genetic differences due to isolation of small segments of the whole. Under such circumstances there is said to be a potential loss of heterozygosity and its accompanying morphological variability, together with potential evolution of the isolated segments along lines divergent from that of the species proper. This appears to be a satisfactory explanation of the condition in *C. aurea*, but experimental data to support this view are insufficient. Although colony-to-colony variation can be demonstrated statistically in *C. flavula*, this does not carry over into any recognizable regional pattern of variability. I hope to have opportunity to discuss this question more fully in a future study.

Another type of variability common to many plant species is most striking in *C. sempervirens* and *C. micrantha*. The conditions under which the particular

plant grows affect gross size and form to a marked degree. For example, plants subjected to abnormally dry conditions often are dwarfed; those growing in shade have fewer branches, more delicate-textured leaves and more slender stems. When plants of *C. micrantha* grow closely crowded together they are less branched and a higher percentage of normal flowers is developed.

The probability of interspecific hybridization in nature is limited to *C. aurea*, *C. micrantha* and *C. curvisiliqua*. These species seem to be closely related, and the possibility or even probability of hybridization among them must be considered. Evidence for this is at present inferential and is based upon plants of intermediate character collected in southern Missouri, Oklahoma, and Texas. Controlled crosses between these species are necessary to supply affirmative or negative evidence of potential hybridization in nature.

In adopting the category of subspecies, I have attempted to maintain its usage in the strictest sense. According to this usage, each subspecies has a discrete or nearly discrete distribution of its own within that of the species as a whole. One may have potential overlap in situations where the habitats favored by the subspecies themselves overlap or intergrade. In instances where two or more elements of the species have been isolated historically by some barrier subsequently removed, the elements may again intermingle along their zone of contact providing they are still interfertile.

The second attribute of a subspecies in *Corydalis* is minor but perceptible morphological differentiation. The subspecies are not always mutually exclusive on morphological grounds, but each has a norm of variability which differs from that of other subspecies. It sometimes becomes a matter of judgment as to whether to describe two closely related elements as species or subspecies. There is no hard-and-fast rule which will be universally applicable due to the fundamental nature of speciation.

Chromosomal Complements

The basic chromosome number in *Corydalis* is 8 in species, all European, so far reported, with a single exception having a probable basic number of 7. There is evidence of the occurrence of polyploidy in two species, but the data are too scanty to justify generalization.

Species	Reported by	n	2n
C. bulbosa	Maude[7]	—	24
C. cava	Tischler[8]	8	—
C. lutea	Kellet[9]	—	56?
C. pumila	Nemec[10]	—	16

[7] Maude, in New Phyt. **39**:18. 1940.
[8] Tischler, in Biol. Centralbl. **48**:343. 1928; Planta **8**:696. 1939.
[9] Kellet, acc. to Darlington & Janaki, Chromos. Atlas Cult. Pl. p. 69. 1945.
[10] Nemec, acc. to Tischler, in Planta **8**:695. 1929.

In two American species which I examined, the diploid number has been tentatively established as 16. I hope that a further report on American species will be possible when data from material now under study are compiled.

Alkaloidal Properties

The alkaloidal properties of a large number of fumariaceous and papaveraceous species have been reported by Manske[11]. American species of *Corydalis* investigated have been *C. Caseana* (ssp. *Caseana*), *C. Scouleri*, *C. aurea* (ssp. *aurea*), *C. aurea* ssp. *occidentalis* (as *C. montana*), *C. micrantha* (ssp. *australis*?), *C. crystallina* and *C. sempervirens*. It is of interest to taxonomists that each species was found to contain a particular set of alkaloids, some of which are common to other species but not in the same combinations.

Manske has drawn certain conclusions about interspecific relationships which are substantiated on morphological grounds. For example, from a chemical standpoint, he agrees that *C. micrantha* and *C. crystallina* are species distinct from *C. aurea*. However, he treats *C. aurea* ssp. *occidentalis (C. montana)* as a distinct species, a view that I am not able to support on the basis of comparative morphology. Manske's work has gone a long way in confirming for this group an assumption that perhaps is sometimes unwarranted, that is, that physiological differentiation may accompany morphological differentiation, even in lower systematic categories. It would be of great interest to the taxonomist to know whether changes in alkaloidal properties are present in widely separated geographical segments of a species in which little or no morphological differentiation is present.

Economic Importance

In so far as is known, the species of *Corydalis* are not of great economic importance. According to collectors' notes, the plants are utilized by the Zuñi Indians of the Southwest, but to what extent or purpose is unknown to me. As a forage for livestock, they are of no importance both because of their relative scarcity and the apparent unpalatibility of the foliage. On account of their high alkaloidal content, it is probable that they are distasteful to livestock as well as toxic if eaten in quantity.

Many species of *Corydalis* have been grown in gardens as much for their value as curiosities as for their intrinsic decorativeness. Of the American species, *C. Caseana* ssp. *Brandegei* and ssp. *Cusickii* are especially recommended for trial. Both are handsome plants in nature, but greatly restricted in habitat. *C. Scouleri*, *C. aurea*, and *C. sempervirens* have been under cultivation in European gardens in the past.

[11] Series of papers in Can. Jour. Res. Ser. B, beginning with 7:258–264. 1932, and still continuing.

GEOGRAPHICAL DISTRIBUTION

The genus *Corydalis* is confined almost exclusively to the northern hemisphere. Its center of diversity is in Eurasia, there being several times the number of species there as are found in North America. In North America, the greatest number of species are concentrated in eastern Oklahoma and adjacent Texas, Arkansas, and Missouri, all species found there being placed in Section EUCORYDALIS. The closest affinities of each of the sections represented in North America are, however, with their Asiatic and European counterparts, and not with each other. Problems of the limits of distribution of the American species are discussed individually in the taxonomic section which follows.

ACKNOWLEDGMENTS

I am greatly indebted to the Missouri Botanical Garden and to its director, Dr. G. T. Moore, for the use of its library and herbarium facilities during the course of this study. I am especially grateful to Dr. J. M. Greenman and Dr. R. E. Woodson for their help and guidance.

I wish to extend my thanks to the curators of the several herbaria who have permitted me to study the material located at their institutions. However, in order to conserve space in this paper it has been necessary to omit detailed lists of specimens examined with the exception of the material from Mexico, Canada, Alaska, and that of *C. micrantha* ssp. *texensis* first described in this paper. The disposition of all numbered and many unnumbered collections viewed in the course of this study may be ascertained by reference to the Index to Exsiccatae. For the information of curators of herbaria and other interested persons, citation of authenticated specimens for each county listed may be found in the original manuscript which is deposited in the library of Washington University, St. Louis, Missouri. Following is a list of the herbaria, together with the abbreviations adopted. Material at each of these herbaria has been viewed and annotated by me.

CA—Herbarium, Colorado Agriculture and Mechanics College.
CAS—Herbarium, California Academy of Sciences.
CIUC—Clokey Herbarium, University of California.
D—Dudley Herbarium, Leland Stanford University.
DU—Herbarium, Duke University.
G—Gray Herbarium, Harvard University.
IH—Intermountain Herbarium, Utah State Agricultural College.
M—Herbarium, Missouri Botanical Garden.
NMA—Herbarium, New Mexico College of Agriculture and Mechanic Arts.
NY—Herbarium, New York Botanical Garden.
RM—Rocky Mountain Herbarium, University of Wyoming.
T—Herbarium, Tulane University.
UA—Herbarium, University of Arizona.

UC—Herbarium, University of California.
UM—Herbarium, University of Minnesota.
UO—Herbarium, University of Oklahoma.
US—United States National Herbarium.
UT—Herbarium, University of Texas.
WS—Herbarium, State College of Washington.

Taxonomy

CORYDALIS Vent. Choix de Pl. *t. 19.* 1803, *nom. conserv.*, exclusive of *Corydalis fungosa* Vent.; not Medik.

[*Capnoides* Tourn. Inst. Rei Herb. 423, *t. 237.* 1719].
Fumaria L. Sp. Pl. 2:700. 1753, in part.
Capnoides Adans. Fam. Pl. 2:431. 1763, *nom. rejic.*
Neckeria Scop. Introd. Hist. 313. 1777, *nom. rejic.*
Pseudo-Fumaria Medik. Phil. Bot. 1:110. 1789, *nom. rejic.*
Pistolochia Bernh. Syst. Verz. Pfl. 57. 1800; not Raf.
Borckhausenia Gaertn. ex Mey. & Scherb. Oekon.-Tech. Fl. Wett. 3:4. 1801.
Odoptera Raf. Cat. 15. 1824.
Capnites Dumort. Fl. Belg. 117. 1827.
Bulbocapnos Bernh. in Linnaea 8:469. 1833.
Sophorocapnos Turcz. in Bull. Soc. Nat. Mosc. 21^1:570. 1848.
Cryptoceras Schott & Kotschy, in Oester. Bot. Wochenbl. 4:121. 1854.
Corydallis Aschers. Fl. Prov. Brand. 2:9. 1864.
Capnodes Ktze. Rev. Gen. 1:13. 1891.

Annual, biennial or perennial herbs from a tap root, tuberous root or rhizome; stems monopodial or sympodial; leaves simple or pinnate, the pinnae deeply once or twice divided and incised; inflorescence a panicle or raceme, terminal, bracteate; flowers bilaterally symmetrical; sepals 2, scarious, often fugacious; petals 4, free or somewhat coherent at the base, in two whorls of two petals each; outer petals dissimilar, one spurred, the other sometimes gibbous at the base, both more or less distinctly keeled or hooded at the apex; inner petals similar, connate at the apices, clawed; stamens in two groups or phalanges opposite the outer petals, each phalange with three anthers, the outer two of which are monothecal, the central dithecal; phalange opposite the spurred petal having a distinct glandular spur which is adherent to the inner surface of the petal spur except at the tip; stigma persistent, flattened, sometimes 2-lobed, with 4–8 papillary stigmatic surfaces; style distinct, slender; fruit a bicarpellate, many-seeded capsule, with two sterile valves and two persistent placentae; seeds having a distinct chalazal appendage or caruncle, smooth or variously decorated under magnification.

Standard Species: C. SEMPERVIRENS (L.) Pers. Syn. Pl. 2:269. 1807.

KEY TO THE SECTIONS

A. Perennial from a rhizome or tuberous root; leaf blades pinnate or simple; flowers never yellow; fruits oblongoid to obovoid, reflexed upon erect or spreading, straight pedicels; stigma approximately rectangular or triangular, as long as broad or longer.

B. Rank-growing, hydrophilous species of western United States; rhizome and roots large and fleshy; leaf blades pinnate, the pinnae

once or twice pinnatifid or incised; flowers pink or white; stigma rectangular, or if triangular, narrowest at the apex.....Section I. RAMOSO-SIBIRICAE (p. 198)

BB. Low-growing species of the far north; roots small, tuberous, usually bifurcate; leaf blades simple, once ternately divided, the segments incised; flowers blue or purplish-blue; stigma triangular, broadest at the apex .....Section II. PES-GALLINACEUS (p. 207)

AA. Annual or biennial, with a somewhat succulent root; leaf blades pinnate, the pinnae once or twice pinnatifid or incised; flowers yellow (except in sp. 4); fruits narrowly to broadly linear, never reflexed upon the straight or curved pedicels; stigma approximately rectangular, broader than long (except in sp. 4).....Section III. EUCORYDALIS (p. 209)

SECTION 1. **Ramoso-sibiricae** (Fedde) G. B. Ownbey, stat. nov.

Ramoso-sibiricae Fedde, in Engler & Prantl, Nat. Pflanzenf. ed. 2. 17b:131. 1936, as subsection.

KEY TO THE SPECIES AND SUBSPECIES

A. Stem leaves about 3; primary axis of inflorescence with about 25 flowers; flowers pink, the inner petals not tipped with deep red or purple; outer petals having no wing margin, the hood generally having a very high crest; stigma approximately triangular, narrowest at the apex, about as broad as long; fruit obovoid; seeds about 3.5 mm. in diameter, distinctly papillose under magnification; coastal Washington, Oregon, and Vancouver Island.....1. *C. Scouleri*

AA. Stem leaves 3–5; primary axis of inflorescence often with 50 or more flowers; flowers pink to white, the inner petals always tipped with deep red or purple; outer petals usually having a well-developed wing margin, the hood with a low or obsolescent crest; stigma approximately rectangular, longer than broad; fruit oblongoid, elliptical, rarely obovoid; seeds about 2.5 mm. in diameter, obscurely papillose under magnification.

B. Plants about 10 dm. tall; wing margin of the outer petals lacking or narrow, the unspurred outer petal acute; California.....2. *C. Caseana* ssp. *Caseana*

BB. Plants 8–20 dm. tall (except ssp. 2b); wing margin of the outer petals moderately to very highly developed, the unspurred outer petal not acute.

C. Outer petals rounded, sometimes mucronulate, the wing margin scarcely folded back upon the hood.

D. Plants mostly 10–15 dm. tall; flowers pink or white; outer petals mucronulate; Colorado.....2a. *C. Caseana* ssp. *Brandegei*

DD. Plants mostly 4–10 dm. tall; flowers white; outer petals occasionally barely retuse, not mucronulate; Utah.....2b. *C. Caseana* ssp. *brachycarpa*

CC. Outer petals emarginate, the wing margin folded back upon the hood.

D. Inflorescence not profusely branched; spurred petal 18–24 mm. long; wing margin very highly developed, not erose; northeastern Oregon and southern Idaho.....2c. *C. Caseana* ssp. *Cusickii*

DD. Inflorescence profusely branched; spurred petal 16–20 mm. long; wing margin moderately developed, minutely erose; northern Idaho.....2d. *C. Caseana* ssp. *hastata*

As here understood this section includes only two species, *C. Scouleri* of coastal Oregon, Washington, and Vancouver Island, and *C. Caseana* of widespread but sporadic occurrence in many mountainous districts of western United States.

Under *C. Caseana* are included several variants which hitherto have been regarded as distinct species. These variants are essentially identical with respect to coloration of the flowers and detailed morphology of the inner petals, stigmas, fruits, and seeds. They differ appreciably in what are better considered as minor characters, such as the development of a wing margin on the outer petals, length of spur, and length of pedicel. The leaves and gross size of the plants vary to some extent among the different elements of the species, but the taxonomic value of these must be discounted as about the same type and degree of variability are found in other species of the genus.

Corydalis Caseana is an excellent example of the type of morphological divergence commonly met with when component parts of a species are isolated geographically. The subspecies might be thought of as incipient species whose modified genetic make-up and consequent morphological divergence have not yet reached the species level. In another sense they might be thought of as remnants of a species which through isolation have lost a large portion of the genetic variability present in the ancient stock.

The members of this section have well-defined habitat requirements, any deviation from which is sufficient to prevent survival. The plants grow in or near a continuous source of fresh, running water, in springs, along small creeks, and in the case of ssp. *Brandegei* also in wet, open, subalpine forests. All require considerable sunlight for best development, but at the same time will tolerate some shade. Plants growing in the sun tend to have smaller, more firmly textured leaves. *C. Scouleri* grows at elevations of sea level to about 2500 feet. The subspecies of *C. Caseana* grow at elevations of 3000–11,000 feet.

The time required for these plants to reach flowering size is not known. At one locality I have seen seedlings of at least three size classes. These classes very likely correspond to age intervals of one year, yet the largest of the seedlings was still relatively small. It therefore seems probable that these plants do not attain flowering size until they are four years or more old.

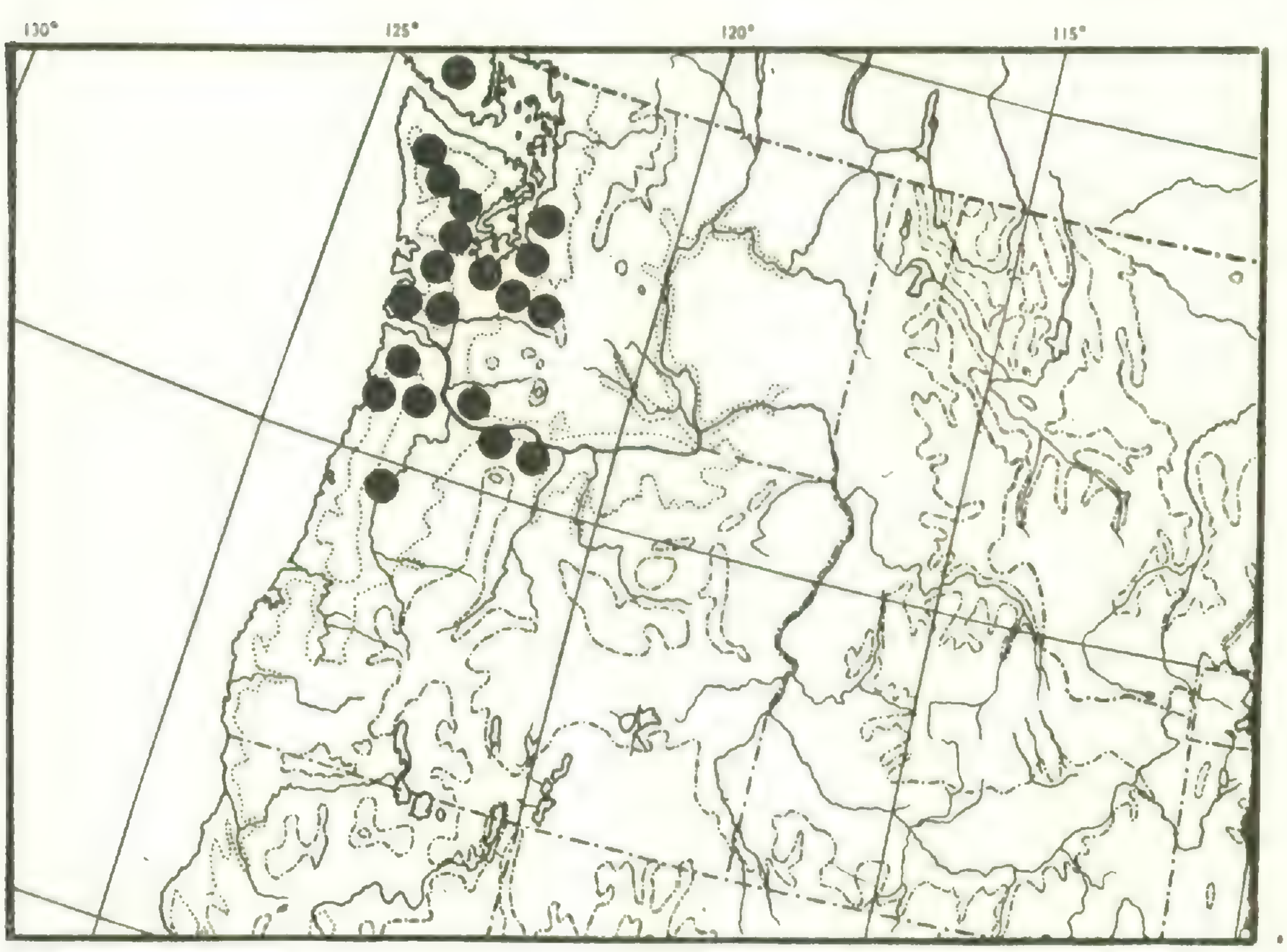
1. C. SCOULERI Hook. Fl. Bor. Am. **1**:36. *t. 14.* 1829.

Corydalis macrophylla Nutt. apud Torr. & Gray, Fl. N. Am. **1**:69. 1838; Torr. & Gray, l. c. 665. 1840, as syn.
Capnodes Scouleri Ktze. Rev. Gen. **1**:15. 1891.
Corydalis Allenii Fedde, Rep. Spec. Nov. **10**:478. 1912.
Capnoides Scouleri Thornber ex Fedde, in Engl. & Prantl, Nat. Pflanzenf. ed. 2. **17b**:133. 1936, nom. nud. in synon.

Perennial from a rhizome; stems 1 or more, usually 5–10 dm. tall, branched above; stem leaves widely divergent, about 3, very long-petiolate; blades pinnately, more or less ternately, compound, 1 dm. or more long and broad, the primary segments once or twice pinnatifid or incised, the ultimate segments variable, sometimes broadly elliptical or less commonly ovate or obovate with rounded apices, or sometimes narrowly elliptical with acute apices, but more often intermediate, 1–8

cm. long, 0.5–4.0 cm. broad, minutely apiculate; inflorescence not strongly monopodial, consisting of 1 or more simple racemes or sparingly branched panicles arising from the axils of the stem leaves, each raceme usually with fewer than 25 flowers; bracts obscure, the lowermost narrowly elliptical, the upper much reduced, linear; pedicels erect, 2–5 mm. long; sepals ovate or broadly lanceolate, laciniate or toothed, 1–2 mm. long, deciduous at anthesis; flowers light to deep pink, the inner petals not tipped with purple; spurred petal usually somewhat arcuate, 20–25 mm. long, the lanceolate spur 14–20 mm. long, the regular crest moderately to very highly developed, extending to and beyond the acute tip of the hood, wing margin absent; unspurred outer petal 12–15 mm. long, naviculate, the crest similar to that of the spurred petal; inner petals usually 9–11 mm. long, the blade much broader at the apex, the slender claw equalling the blade in length; stamen spur one-half to two-thirds the length of the petal spur, bent or hooked at the apex; stigma roughly triangular, the width at the lower lobes about the same as the length along the medial line; style slender, about 3 mm. long; fruit obovoid, 10–15 mm. long, 4–5 mm. broad; seeds black, about 3.5 mm. in diameter, conspicuously papillose under magnification.

This species is limited in distribution. It is found in wet, cool habitats of northwestern Oregon, northward to Vancouver Island. Morphologically, it is most easily distinguished from *C. Caseana* by its generally highly developed crest and absence of a wing margin on the outer petals. The obovoid fruits most typical of



Map 1. Distribution of *Corydalis Scouleri* Hook.

this species are rarely approached in *C. Caseana*, and its approximately triangular stigma may be contrasted with the nearly rectangular stigma found in that species. Finally, the seeds of *C. Scouleri* are considerably larger and more distinctly papillose.

Within the species there is considerable morphological variability, especially with respect to the leaves. The very small, narrowly elliptical ultimate leaf segments found on some specimens are in part the basis for Fedde's proposed segregate, *C. Allenii*, which I cannot maintain on valid grounds. *C. Scouleri* also is variable with regards to its flowers, particularly in length of spur, amount of curvature of the spurred petal, development of the crest, and gross size. When considered against the background of the species as a whole these variants lose their systematic significance. As possible examples of population variability potentialities of the species from locality to locality they are of considerable interest.

Moist, shady woods, especially along water courses; Vancouver Island, western Washington and northwestern Oregon at elevations of sea-level to about 3500 feet. Flowers about April 15 to June 15; fruits about May 15 to July 30.

BRITISH COLUMBIA: Vancouver Island.

WASHINGTON: Clallam, Clark, Grays Harbor, Jefferson, King, Mason, Pacific, Pierce, Thurston, and Wahkiakum counties.

OREGON: Benton, Clackamas, Clatsop, Columbia, Hood River, Marion, Multnomah, Tillamook, and Washington counties.

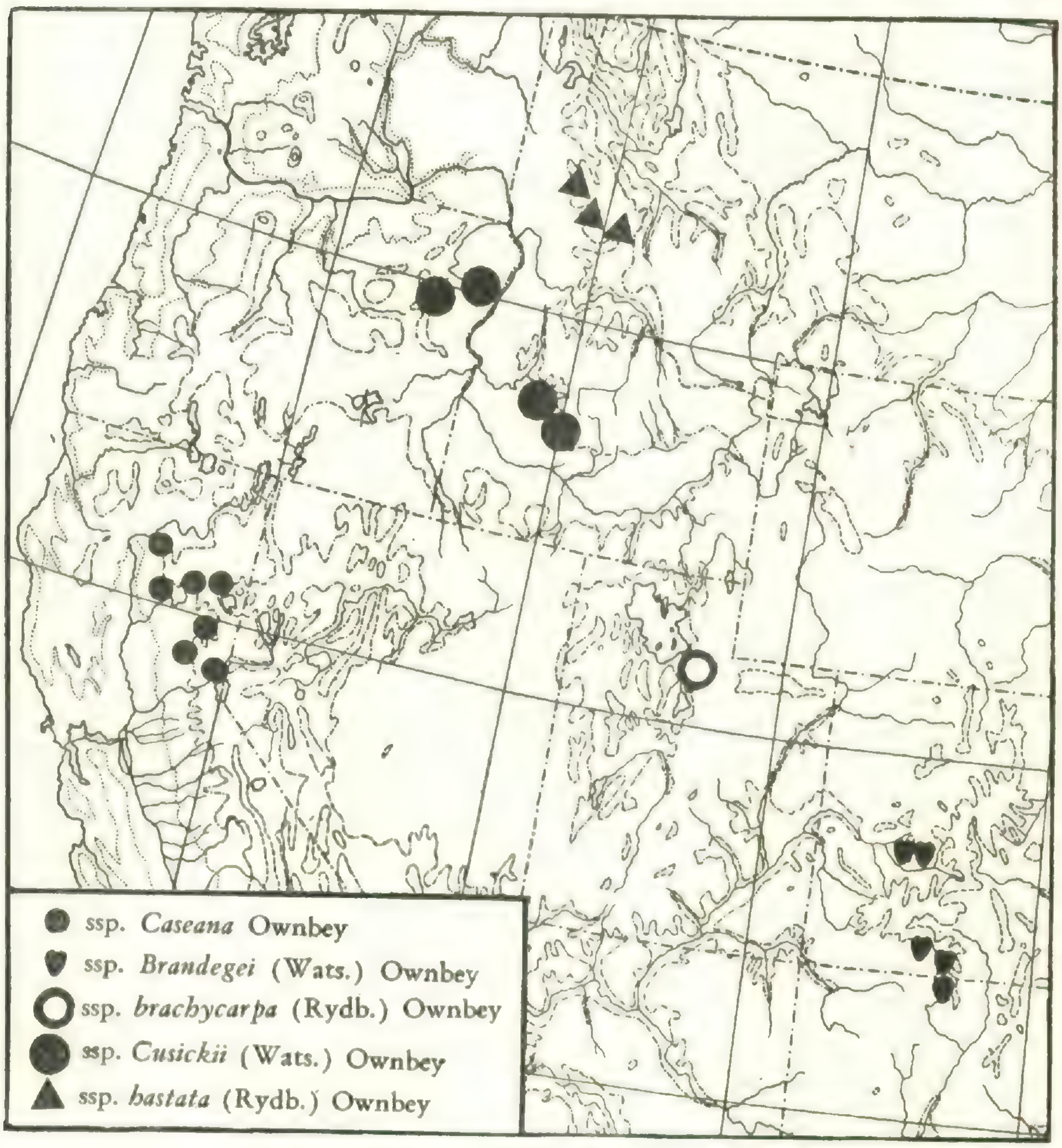
2. C. CASEANA Gray ssp. **Caseana** G. B. Ownbey, stat. nov.

Corydalis Caseana Gray, in Proc. Am. Acad. **10**:69. 1874.
Corydalis Bidwelliae Watson, Bot. Calif. **2**:429. 1880.
Capnodes Bidwellianum Greene, Fl. Fran. 280. 1891.
Capnodes Caseanum Greene, l. c. 1891.
Capnodes Caseanum Ktze. Rev. Gen. **1**:14. 1891.

Glaucous perennial; stems 1–several, generally 10 dm. or less in height; stem leaves about 5, pinnate, the primary segments again once or twice pinnatifid or deeply incised; ultimate segments narrowly to broadly elliptical, mostly 1–2 cm. long, apiculate; inflorescence paniculate, consisting of a strong numerous-flowered central axis and 1 to several shorter, fewer-flowered lateral axes, these often again branched at the base; bracts inconspicuous, usually narrowly elliptical, rarely broader in outline, the lowermost about 10 mm. long, greatly reduced upward; pedicels semi-erect, 3–5 mm. long; sepals variable, sometimes with a broad base and a very long-attenuated central lobe, sometimes orbicular and denticulate at the margin, sometimes otherwise, 2–4 mm. long, rarely persisting through anthesis; flowers light pink or probably also white, the inner petal tips reddish-purple; spurred petal often curved, usually 16–22 mm. long, rarely longer, the spur gradually to rapidly tapered to the blunt apex, 12–16 mm. long, the hood crested, the crest regular or denticulate, rarely obsolete, extending to and beyond the acute tip of the petals, the wing margin, if present, narrow, regular or more or less denticulate and not folded back toward the hood; unspurred outer petal 10–12 mm. long, the crest and margin similar to that of the spurred petal; inner petals

usually 9–10 mm. long, the claw 3–5 mm. long; stamen spur one-half to three-fourths the length of the petal spur; stigma approximately rectangular, with 8 papillary stigmatic surfaces; style about 3 mm. long; fruit oblong, 10–15 mm. long, 3–4 mm. broad; seeds dark brown to black, minutely papillose under magnification, about 2.5 mm. in diameter.

Morphologically, the subspecies is best distinguished by its narrow or obsolete wing margin, its generally narrower, curved spurred petal, and acute apices of the outer petals. It is probably most closely similar to ssp. *Brandegei* from which it differs appreciably in the smaller gross size of the plants, smaller flowers, and narrower petal margins. The variant named *C. Bidwelliae* by Watson is of no



Map 2. Distribution of *Corydalis Caseana* Gray.

systematic importance. Leaflet size, petal margin, crest and slenderness of the spur upon which Watson's proposed species was based vary to some extent even at a single locality.

This plant has been collected as far south in California as Truckee, by Sonne, but there are no recent collections from this area.

Very moist, often shady situations, in springs and on gravel bars, in and along streams; southeastern Shasta County southward and eastward to Placer County, California, at elevations of about 4000–6000 feet. Flowers from about June 1 to July 30; fruits from about July 1 to September 1.

CALIFORNIA: Butte, Lassen, Placer, Plumas, Sierra, and Tehama counties.

2a. C. CASEANA Gray ssp. **Brandegei** (Wats.) G. B. Ownbey, stat. nov.

Corydalis Brandegei Watson, Bot. Calif. 2:430. 1880.
Capnoides Brandegei Heller, Cat. N. Am. Pl. 55. 1898.

Glaucous perennial; stems 1–several, 5–15, mostly 10–15, dm. or more in height; stem leaves about 5, the lowermost sometimes 10 dm. long, pinnate, the pinnae once or twice pinnatifid or deeply incised, the ultimate segments mostly elliptical, 1–5 cm. or more long, apiculate; inflorescence paniculate, consisting of a central numerous-flowered axis and often 1–several fewer-flowered secondary axes, these sometimes again branched; bracts inconspicuous, narrowly elliptical to linear, much reduced and minute upward; pedicels semi-erect, about 5 mm. in length, up to 10 mm. in fruit; sepals 2–3 mm. long, ovate or orbicular, the margin irregularly toothed; flowers light pink to white, the inner petals tipped with deep red or purple, inverted, the spur often nearly upright along the raceme; spurred petal 18–25 mm. long, the spur 12–16 mm. long, the hood crested, the crest low and regular, extending to and beyond the rounded apex of the petal to form a short beak, the wing margin broad, scarcely folded back toward the hood; unspurred outer petal about 12 mm. long, the crest and wing margin similar to that of the spurred petal; inner petals 10–12 mm. long, the claw 4–5 mm. long; stamen spur about two-thirds the length of the petal spur; stigma approximately rectangular, with 8 papillary stigmatic surfaces; style about 3 mm. long; fruit oblong, 15–18 mm. long, about 5 mm. broad; seeds dark brown to black, about 2.5 mm. in diameter, minutely papillose under magnification.

This subspecies is distinguished most easily on the basis of the wing margin, which is broad, regular, not retuse at the apex, and not appreciably folded back upon the hood as in ssp. *Cusickii* and ssp. *hastata*. It sometimes appears so when the flowers are distorted in pressing. The manner in which the low, regular crest extends beyond the rounded apex is characteristic. Occasionally the spur is nearly erect and the fruits, when mature, reflexed nearly to the pedicels. This situation is found especially in plants from the southern portion of the range.

Subspecies *Brandegei* is very abundant in Colorado from the summit of Wolf Creek Pass, Mineral County, for approximately 4 miles down the west side, at elevations of about 10,000–10,800 feet. Only a few plants are present on the

east side of the pass. At this site the flowers are uniformly pinkish-lavender in color. At similar elevations in Kebler Pass, Gunnison County, the plant also is abundant, especially on the west slope for at least two miles from the summit. The plants are essentially identical to those at Wolf Creek Pass except with respect to flower color. Here there is a preponderance of very light, nearly white-flowered individuals.

Very moist, subalpine situations, especially along water courses, at elevations of about 8,000–11,000 feet; Gunnison and Delta counties, Colorado, southward to northern Rio Arriba County, New Mexico. Flowers from about June 10 to August 10; fruits from about July 10 to September 10.

Colorado: Archuleta, Conejos, Delta, Gunnison, Hinsdale, and Mineral counties.
New Mexico: Rio Arriba County.

2b. C. Caseana Gray ssp. **brachycarpa** (Rydb.) G. B. Ownbey, stat. nov.

Capnoides brachycarpum Rydb., in Bull. Torr. Bot. Club 34:426. 1907.
Corydalis brachycarpa Fedde, Rep. Spec. Nov. 10:315. 1912.

Glaucous perennial; stems 1–6, 4–10 dm. tall; leaves 3–5, the lower ones long-petiolate, pinnate, the pinnae once or twice pinnatifid or incised; ultimate leaf segments elliptical, acute at both ends, usually 1–3 cm. long and 0.4–1.0 cm. broad, minutely apiculate; inflorescence paniculate, consisting of a stout central axis and often one or more secondary axes; bracts linear, the lower ones about 15 mm. long, much reduced above; pedicels stout, spreading to semi-erect, about 5 mm. long at flowering time, up to 10 mm. or more long at fruiting time; sepals ovate or broadly lanceolate, more or less undulate or toothed at the margin, 3–5 mm. long, sometimes persisting through anthesis; flowers white, the inner petals tipped with deep red or purple; spurred petal 18–22 mm. long, the spur straight, gradually narrowed to the blunt apex, 9–12 mm. long, the wing margin broad, undulate, stiff, not appreciably folded back toward the hood, rounded at the apex, occasionally barely retuse, the crest obsolescent or lacking; unspurred outer petal 12–14 mm. long, the margin and crest similar to that of the spurred petal; inner petals 9–11 mm. long, the claw about 4 mm. long; stamen spur one-half to two-thirds as long as the petal spur; stigma approximately rectangular, with 8 papillary stigmatic surfaces; style about 3 mm. long; fruit oblong in outline, about 12 mm. long and 4 mm. broad; mature seeds not seen.

Subspecies *brachycarpa* is a well-marked unit. It is best distinguished morphologically on the basis of the broad, spreading wing margin of the outer petals which are commonly neither acute-tipped nor emarginate, but rounded, at the apex. The broad margin is very well developed even in the bud. The plant possibly is closest to ssp. *Cusickii*, but in addition to the above-mentioned differences, it is only about one-half as large. The leaves are very similar to those of ssp. *Cusickii* as found in Oregon.

The name *brachycarpa* is something of a misnomer if it was intended to call attention to a fruit difference between this and other members of the complex.

The normal fruits, although perhaps smaller than those ordinarily found in other subspecies, are in no way significantly different. It is probable that the name was applied because of a misinterpretation of the swollen fruits very commonly found on living plants. All such fruits examined were found to contain an insect larva, the adult counterpart of which has not been identified. The stimulation of growth of pathogenic tissue results in a globose, spongy, abnormal, sterile fruit. A similar situation is not uncommon in *C. aurea*.

This subspecies is of very limited distribution, and it is possible that the adult population numbers no more than a few hundred individuals.

On gravel bars along stream courses at elevations of about 8500–10,000 feet; Wasatch Mountains, Salt Lake and adjacent Utah counties, Utah. Flowers from about July 1 to July 30; fruits from about July 30 to August 30.

UTAH: Salt Lake and Utah counties.

2c. C. CASEANA Gray ssp. **Cusickii** (Wats.) G. B. Ownbey, stat. nov.

Corydalis Cusickii Watson, Bot. Calif. 2:430. 1880.
Capnoides Cusickii Heller, Cat. N. Am. Pl. 55. 1898.
Corydalis Hendersonii Fedde, Rep. Spec. Nov. 12:278. 1913; not Hemsl.
Corydalis idahoensis Fedde, l. c. 16:195. 1919.

Glaucous or green perennial; stems 1–several, 8–15 dm. tall; leaves 4–6, pinnate, the pinnae once or twice pinnatifid or deeply incised; ultimate leaf segments usually narrowly, sometimes broadly, elliptical, apiculate, 1–5 cm. long, 0.5–1.5 cm. broad; inflorescence paniculate, consisting of a stout central axis bearing numerous flowers and 1–several shorter, fewer-flowered secondary axes; lowermost bracts very narrowly to broadly elliptical or obovate, often 15 mm. long, much reduced and usually linear above; pedicels spreading, 5–10 mm. long at flowering time, often up to 15 mm. long at fruiting time; sepals ovate to lunate, often toothed or laciniate, 2–4 mm. long; flowers white or tinged with pink, the inner petals tipped with deep red or purple, the apices of the outer petals widely divergent; spurred petal 18–24 mm. long, the spur generally straight, 10–14 mm. long and not rapidly tapering to the blunt apex, the crest, when present, low and inconspicuous, the wing margin extremely broad, deeply notched at the apex and folded back upon the hood; unspurred outer petal 12–15 mm. long, the margin similar to that of the spurred petal; inner petals 9–11 mm. long, the slender claw about 4 mm. long; stamen spur straight, one-half to three-fourths the length of the petal spur; stigma approximately rectangular, with 8 papillary stigmatic surfaces; style 3–4 mm. long; fruit oblong-elliptical, 10–15 mm. long, 4–5 mm. broad; seeds dark brown, minutely papillose under magnification, about 2.5 mm. in diameter.

The highest development of the wing margins of the outer petals found anywhere within the species is present in ssp. *Cusickii*. This and the long pedicels are its most distinctive features. The wing margin and emarginate apex is emulated on a much lesser scale by ssp. *hastata*. Both ssp. *brachycarpa* and ssp. *Brandegei* have broad margins, but they never are greatly emarginate at the apex and the

margins are stiffer and never appreciably folded back upon the hood when the flowers are fresh.

This plant was described by Watson from material collected by Cusick in the Wallowa and Blue mountains of northeastern Oregon. It still is collected occasionally in the Wallowa Mts. and is present in some abundance above Cornucopia. It has been collected a few miles above Sumpter in the Blue Mts. and if it is at all abundant in this area it is at this point or further south. In Idaho, a variant with broader bracts, generally broader leaflets, and less-branched inflorescence is common in some localities. The Idaho form was described as *C. Hendersonii* by Fedde. It is found along the tributaries of the South, Middle and North Forks of the Boise River and the South Fork of the Payette River at known elevations of 5000–7500 feet. It does not often occur along the larger streams. On a hillside about 6 miles northeast of Rocky Bar, Elmore County, there is a pure stand covering approximately one-half acre. The plant here reaches its maximum development.

Growing in and along springs and small streams at elevations of about 5000–7500 feet; mountains of southwestern Idaho and northeastern Oregon. Flowers from about June 15 to July 30; fruits from about July 1 to August 15.

IDAHO: Boise, Camas, Elmore, and Valley counties.

OREGON: Baker and Union counties.

2d. C. CASEANA Gray ssp. **hastata** (Rydb.) G. B. Ownbey, stat. nov.

Capnoides hastatum Rydb., in Bull. Torr. Bot. Club **34**:426. 1907.
Corydalis hastata Fedde, Rep. Spec. Nov. **10**:315. 1912.
Corydalis Cusickii var. *hastata* Fedde, l. c. **12**:279. 1913.

Glaucous or green perennial; stems 1–several, 10–18 dm. tall; main stem leaves 3–5, the lower ones widely divergent from the stem, the blade deltoid, pinnate, the pinnae once or twice pinnatifid or deeply incised; ultimate leaf segments broadly elliptical, ovate- or obovate-elliptical, rounded or acute at the ends, usually 1.5–4 cm. long and 0.5–1.5 cm. broad, minutely apiculate, of very thin, tissue-like texture when dry; inflorescence paniculate, delicately and profusely branched, consisting of a main axis and several more or less branched secondary axes; bracts often foliose, ovate to obovate, somewhat reduced above; pedicels about 5 (5–10) mm. long, semi-erect or spreading; sepals about 2 mm. long, usually with an elongate, lanceolate medial lobe and two basal auricles which are often somewhat toothed at the margins; flowers pale pink to white, the inner petals tipped with deep red or purple; spurred petal 16–20 mm. long, the spur 10–12 mm. long, straight or incurved, gradually narrowed toward the broad, blunt apex, the wing margin moderately well developed, reflexed toward the hood, commonly erose, retuse at the apex, the low crest extending over the apex of the hood into a short beak; unspurred outer petal 10–12 mm. long, the margin and crest similar to that of the spurred petal; inner petals 7–9 mm. long, the stout claw about one-third the total length; stamen spur two-thirds to three-fourths as long as the petal spur; stigma approximately rectangular, with 8 papillary stigmatic surfaces; style 2–3

mm. long; fruit oblong, 12–16 mm. long, about 4 mm. broad; mature seeds dark brown, minutely papillose under magnification, about 2.5 mm. in diameter.

Although characterized by numerous morphological differences of greater or lesser value, this plant must be included with *C. Caseana* in the broad sense. It is best distinguished morphologically on the basis of the broadly spreading deltoid leaf blades, the broadly elliptical ultimate leaf divisions, and the profusely branched inflorescence. In floral characters it most closely resembles ssp. *Cusickii,* but differs from it in having considerably smaller flowers with shorter inner petals and outer petals with a much narrower, usually erose wing margin which, as in that subspecies, is reflexed upon the hood and usually is emarginate at the apex. Only in ssp. *Caseana* is the wing margin narrower. The sepals are, indeed, as noted by Rydberg in his original diagnosis, somewhat characteristic. Sepals in *Corydalis* are, however, a very much reduced organ, and there is everywhere considerable variability in outline. I believe that the sepals of ssp. *hastata* cannot justifiably be given much weight as a distinguishing feature.

This subspecies is of limited and as yet not definitely circumscribed distribution. It is found in Idaho from southwestern Shoshone County, southward and eastward to northern Idaho County, probably only at medium elevations. It is especially abundant along Orogrande Creek, Clearwater County. It has been reported from the upper reaches of the Selway River (Moose Creek Trail), but its presence there should be confirmed.

Very wet situations, in and along streams at elevations of about 3000–4000 feet; mountains of northern Idaho. Flowers from about June 15 to July 30; fruits from about July 15 to August 30.

IDAHO: Clearwater, Idaho, and Shoshone counties.

SECTION II. PES-GALLINACEUS

Sect. PES-GALLINACEUS Irmisch, in Abh. Nat. Ges. Halle **6**:273. 1862.

CORYDALIS §. II. *Capnites* DC. Reg. Veg. Syst. Nat. **2**:115. 1821.
Pistolochia Bernh. Syst. Verz. Pfl. 57. 1800.
Bulbocapnos Bernh. in Linnaea 8:469. 1833.

KEY TO THE SPECIES

A single representative in North America.....3. *C. pauciflora*

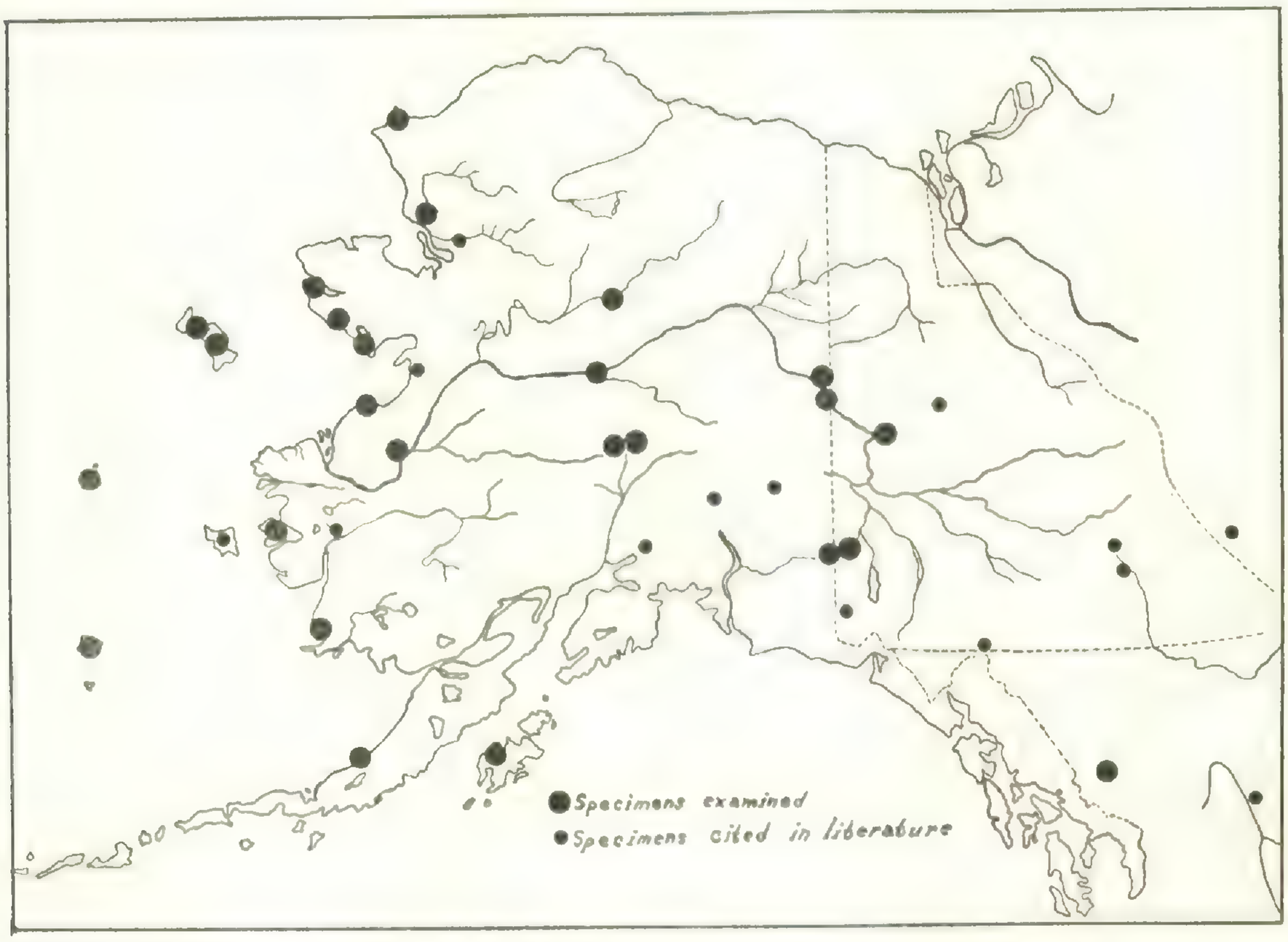
3. C. PAUCIFLORA (Steph.) Pers. Syn. Pl. **2**:269. 1807; Cham. & Schlecht. in Linnaea **1**:560. 1826, not Edgew.

Fumaria pauciflora Steph. ex Willd. Sp. Pl. 3^2:861. 1803.
Corydalis pauciflora γ *parviflora* Regel, in Bull. Soc. Mosc. 34^3:136. 1861.
Capnodes pauciflorum Ktze. Rev. Gen. **1**:14. 1891.
Capnoides pauciflorum Cov. in Brooks et al. Rec. Cape Nome & Norton Bay Reg. 170. 1901.
Corydalis pauciflora var. *Chamissonis* Fedde, Rep. Spec. Nov. **16**:48. 1919.

Perennial; root deep-set, tuberous, usually bifurcate, having a central channel, the fibrous rootlets mostly at the base, accessory buds at the summit 1–several, or lacking; stems usually 1–3, unbranched, erect, mostly 8–20 cm. tall, often with 1–2 basal cataphylls; basal leaves none; stem leaves 2–5, long-petioled, simple, the

blades ternately divided, the segments again incised into 2–4 (usually 3) lobes, the ultimate lobes elliptical; peduncles stout, terminal, with 3-5 inverted flowers crowded at the summit; bracts ovate to obovate, 4–10 mm. long, 3–5 mm. broad, the lowermost larger; pedicels stout, erect, 4–10 mm. long at flowering time, up to 20 mm. long at fruiting time; sepals scarious, fugacious, 1–2 mm. long and broad, variously toothed; flowers blue, often tinged with purple; spurred petal 17–20 mm. long, the hood short and inconspicuous, the low, regular crest extending to or nearly to the obtuse apex of the petal, the wing margin narrow, the spur 7–10 mm. long, abruptly incurved near the blunt apex; spurless outer petal 10–12 mm. long, nearly as broad basally as apically, the apex 1–2 mm. longer than that of the other petals, the crest similar to that of the spurred petal, the margin reflexed; clawed inner petals 8–10 mm. long, the slender claw occupying one-half or more of the total length, the blade obovate; stamen spur clavate, two-thirds to three-fourths the length of the petal spur; stigma triangular, broadest at the 4-lobed apex; fruits reflexed, about 12 mm. long and 5 mm. broad, elliptical to obovate; seeds turgid, black, shiny, essentially smooth under magnification.

This distinctive species is well known to students of boreal floras. It is the only Asiatic species of *Corydalis* whose distribution extends across the Bering Straits into America. It is beyond the scope of this paper to discuss names proposed for variant forms of the species found in Asia. An excellent discussion of the application of the name to the American plant is to be found in Hultén's recent work (Flora of Alaska and Yukon **5**:810. 1945).



Map 3. Distribution of *Corydalis pauciflora* (Steph.) Pers.

In tundra; islands of the Bering Sea and Straits eastward throughout Alaska to the Yukon and northern British Columbia at elevations of sea level to about 3500 feet; also widely distributed in Asia. Flowers from about June 1 to July 15; fruits from about July 1 to August 1.

ALASKA: Ft. St. Michaels, Norton Sound, 1865-66, *Bannister* (G, US); Nome, July, 1890, *Blaisdell 67* (UC); Seal Islands, 1875, *Bryant* (US); Anvik, near the Mission, Lower Yukon River, June 11, 1924, *Chapman 1* (NY); Mission premises, Anvik, without date, *Chapman 28* (G); near Chinik, Seward Peninsula, July 3, 1900, *Collier* (US); St. Paul I., Bering Sea, July 9, 1899, *Coville & Kearney 1810* (US); Port Clarence, July 12, 1899, *Coville & Kearney 1966* (US); Hall I., Bering Sea, July 14, 1899, *Coville & Kearney 2033* (G, US); McKinley Park Sta., Mt. McKinley Nat. Park, June 4, 1932, *Dixon 17* (UC); roadside, Igloo Creek, same locality, June 13, 1932, *Dixon 25* (UC); White River Valley, near the boundary, 1909, *Eaton* (US); St. Matthew I., July 8–13, 1916, *Hanna* (US); on hillside, Goodnews Bay, July 14, 1919, *Harrington 57* (US); St. Paul I., June 30–Aug. 20, 1910, *Heath* (D); Nome, 1914, *Hill 65* (US); wet brook banks, Karluk, June 14, 1901, *Horne* (NY); St. Paul I., Aug. 1, 1897, *Kincaid* (UC); St. Paul I., without date, *MacIntyre* (G); St. Paul I., July, 1892, *Macoun* (NY); St. Paul I., July, 1891, *Macoun* (M, G, US); St. Paul I., June 29, 1914, *Macoun* (NY, US); Cape Lisburne, Aug. 13, 1931, *Mason* (M, UC, NY, G); Iviktook Lagoon, St. Lawrence I., July 10, 1931, *Mason* (UC); Old Man Creek, a branch of the Koyukuk, 4 mi. above camp, near Caribou Mt., July 6, 1901, *Mendenhall* (US); between Yukon River, Nation River, and International Boundary, 1930, *Mertie 60* (US); damp moss in small gulch, open land near Teklanika River, Mt. McKinley Nat. Park, 3600 ft. alt., June 24, 1928, *Mexia 2040* (UC); Golovin Bay, 1881, *Muir 168* (G); moist thicket near headquarters, Mt. McKinley Nat. Park, May 31, 1939, *Nelson & Nelson W-2206* (RM); Nelson I., July 6, 1921, *Palmer 194* (US); St. Paul I., June 10, 1890, *Palmer 178* (US); near Karluk, Kodiak I., June 1, 1897, *Rutter* (D); same locality, May 23, 1897, *Rutter 92* (D); same locality, June 13, 1903, *Rutter 179* (US); same locality, June 14, 1903, *Rutter 206* (M, US); Mt. McKinley Nat. Park, June 13–22, 1937, *Scamman 620* (G); Camp Retreat, June 28, 1886, *Stoney* (US); Anvil Mt., vicinity of Nome, June 29, 1918, *Thornton 319* (US); damp hillside near creek, Tanana, June 14, 1914, *Thousen 6* (DU); St. Paul I., July 9, 1899, *Trelease & Saunders 3872* (M); Hall I., July 4, 1899, *Trelease & Saunders 3873* (M); St. Matthew I., July 15, 1899, *Trelease & Saunders 3874* (M); St. Paul I., July 28, 1895, *True & Prentiss 12* (NY, G, US); Noatak, July, 1929, *Wagner* (US); vicinity of Port Clarence, July 16, 1901, *Walpole 1457* (US); same locality, July 18, 1901, *Walpole 1467* (US); St. Paul I., July, Aug., 1879, *White* (G).

BRITISH COLUMBIA: Mountains near head Iskut River, Cassiar Dist., July 30, 1910, *Preble & Mixter 619* (US).

YUKON: Across Bonanza Creek, Dawson, June 19, 1914, *Eastwood 307* (G, US); 24-mile house, Dawson, June 25, 1914, *Eastwood 380* (CIUC, G, US).

SECTION III. EUCORYDALIS

Sect. EUCORYDALIS Prantl, in Engler & Prantl, Nat. Pflanzenf. 3^2:144. 1889.

Corydalis §. III. *Capnoides* DC. Reg. Veg. Syst. Nat. 2:122. 1821.

KEY TO THE SPECIES AND SUBSPECIES

A. Flowers pink, the petals tipped with yellow, the hood not crested, the claw of the inner petals much longer than the blade; stigma not distinctly 2-lobed, with 4 papillary stigmatic surfaces; fruits erect, very slender, usually 30–35 mm. long; seeds about 1 mm. in diameter; Georgia to Newfoundland, British Columbia, and Alaska ..... 4. *C. sempervirens*

AA. Flowers pale to bright yellow throughout, the claw of the inner petals equalling or shorter than the blade; stigma 2-lobed, each lobe having 3 papillary stigmatic surfaces; seeds 1.5–2.0 mm. in diameter.

B. Spurred petal 7–9 mm. long, the hood having a high, undulate or toothed crest, the spur incurved, about 2 mm. long; fruits broadly linear, usually straight, pendent on very long pedicels; central to eastern United States ..... 5. *C. flavula*

BB. Spurred petal 10–22 mm. long (in normal flowers), the spur not appreciably incurved, usually 4–8 mm. long; fruits erect, on relatively short pedicels (except in sp. 9).

C. Spurred petal 16–22 mm. long, the hood with a very high crest, the wing margin very broad; fruits densely beset with transparent, clavate pustules; southwestern Missouri to central Texas.. 6. *C. crystallina*

CC. Spurred petal 10–18 mm. long, the wing margin moderately broad to narrow; fruits essentially glabrous, although sometimes obscurely granulose along the sutures.

D. Plants often bearing cleistogamous flowers; spurred petal of normal flowers 10–15 mm. long, the hood with a low, regular, undulate or obsolescent crest; seeds about 1.5 mm. in diameter, nearly smooth under magnification.

E. Normal-flowered racemes not greatly exceeding the leaves, often short; spur usually somewhat globose at the tip; fruits often stout, commonly 10–15 mm. long; central United States ..... 7. *C. micrantha* ssp. *micrantha*

EE. Normal-flowered racemes often greatly exceeding the leaves, elongated; spur not globose at the tip; fruits slender, 15–30 mm. long.

F. Stems usually weak and not strongly striate when dry; foliage green to glaucous; fruits 15–20 mm. long; south-central to southern United States ..... 7a. *C. micrantha* ssp. *australis*

FF. Stems usually stout and strongly striate when dry; foliage glaucous; fruits 25–30 mm. long; coastal south Texas ..... 7b. *C. micrantha* ssp. *texensis*

DD. Plants seldom bearing cleistogamous flowers (except in sp. 10); spurred petal mostly 14–18 mm. long; seeds about 2 mm. in diameter, essentially smooth to variously decorated under magnification.

E. Seeds distinctly muricate or muriculate under magnification; central Texas to southern Kansas.

F. Hood crestless or with a moderately well-developed crest; fruits 26–34 mm. long, usually abruptly acute; seeds distinctly muricate under magnification; central and western Texas ..... 8. *C. curvisiliqua* ssp. *curvisiliqua*

FF. Hood with a well-developed crest; fruits 20–25 mm. long, gradually tapered; seeds muriculate under magnification; north Texas to southern Kansas ..... 8a. *C. curvisiliqua* ssp. *grandibracteata*

EE. Seeds never muricate though sometimes muriculate at the margin under magnification.

F. Racemes usually surpassed by the leaves; hood sometimes crested; fruits spreading or pendent, usually 18–24 mm. long; seeds with no ring margin; northern United States to Alaska and southward in the Rocky Mountains to Mexico ..... 9. *C. aurea* ssp. *aurea*

FF. Racemes usually surpassing the leaves (except in sp. 10); hood usually not crested; fruits erect, often incurved; seeds usually having a ring margin.

G. Cleistogamous flowers not present; fruits stout, incurved, usually 12–20 mm. long; southwestern United States and adjacent Mexico..... 9a. *C. aurea* ssp. *occidentalis*

GG. Cleistogamous flowers present; fruits slender, not strongly incurved, 25–30 mm. long; mountains of eastern Mexico..... 10. *C. pseudomicrantha*

With the exception of *C. sempervirens*, all the American species of Section EUCORYDALIS form a coherent group, with *C. flavula* and *C. crystallina* standing somewhat apart. *C. sempervirens*, although properly placed in this section, is quite distinctive in several ways, and conceivably could provide the basis for a subsection. Fedde (in Engler & Prantl, Nat. Pflanzenf. **17b**:129. 1936.) includes all of these species in his subsection EUCAPNOIDES of EUCORYDALIS.

4. C. SEMPERVIRENS (L.) Pers. Syn. Pl. **2**:269. 1807.

Fumaria sempervirens L. Sp. Pl. 2:700. 1753.
Neckeria sempervirens Neck. Elem. Bot. 3:60. 1790.
Fumaria glauca Curt. Bot. Mag. 5: *t. 179*. 1792.
Capnoides glauca Moench, Meth. Pl. 52. 1794.
Capnoides sempervirens Borkh. in Roem. Arch. f. Bot. 1^2:44. 1797.
Corydalis glauca Pursh, Fl. Am. Sept. 2:463. 1816.
Corydalis rosea Eaton, Man. Bot. 79. 1817.
Corydalis annua Hoffmeg. ex Steudel, Nomen. Bot. ed. 2. 1:423. 1841, as syn.
Neckeria glauca Millsp. Fl. W. Va. 327. 1892. (W. Va. Agr. Exp. Sta. Bull. 2),

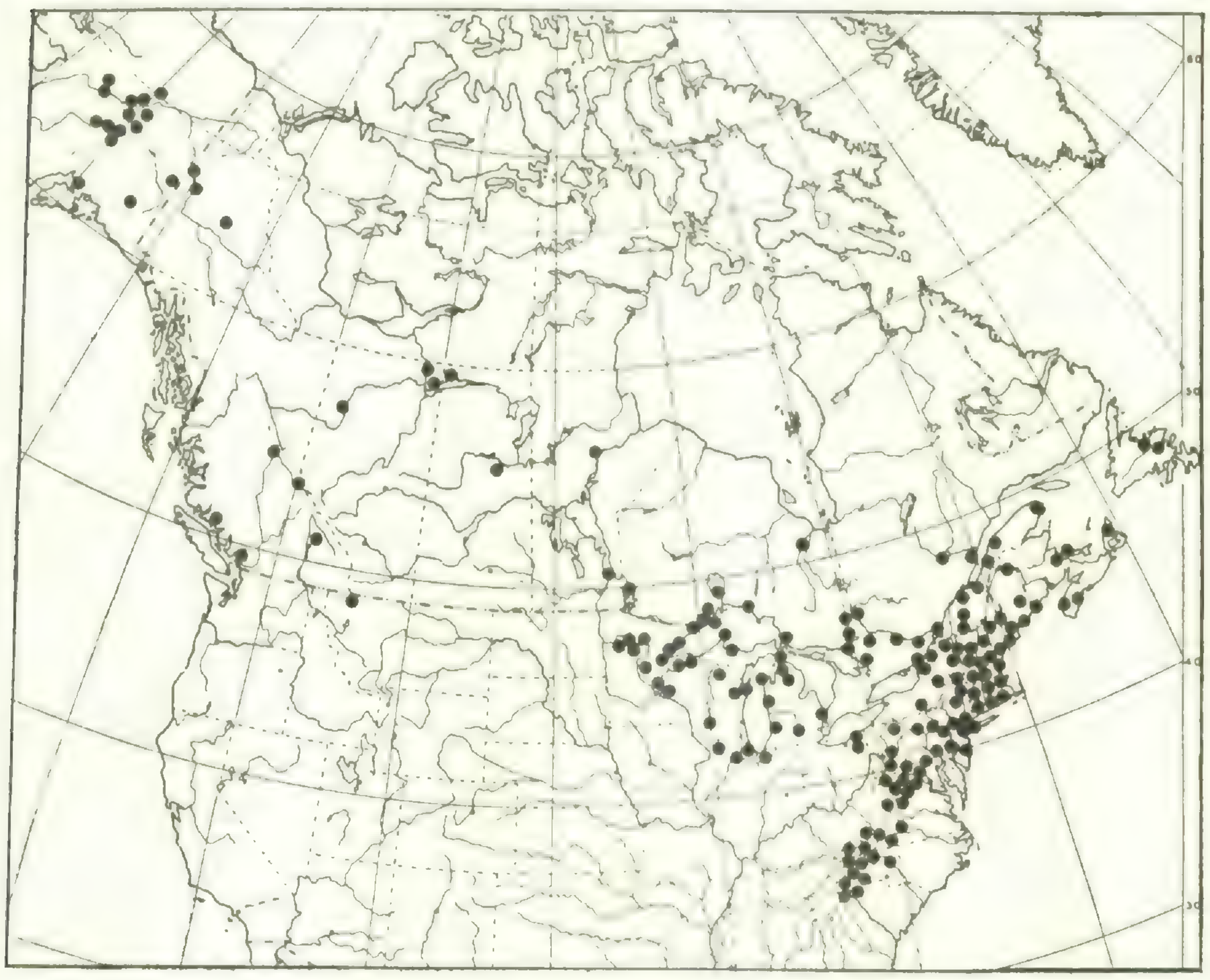
Very glaucous biennial; stems usually 1, approximately 30–80 cm. tall, much branched, erect; earlier cauline leaves long-petioled, crowded; later cauline leaves nearly sessile, much reduced; leaf blades pinnate, the basal with 5 main segments, the upper with 3 main segments, the segments ternately divided, then once or twice incised, the ultimate lobes oblong-elliptical, obtuse, apiculate; inflorescence a raceme or panicle, terminal, each axis 1- to 8-flowered; bracts narrowly elliptical, minute, 2–5 mm. long, 0.5–1.0 mm. broad; pedicels slender, erect, 5–20 mm. long at maturity, successively shorter upward; sepals 3 mm. or less long, ovate, short-attenuate, white or tinged with pink; flowers pink, the petals tipped with yellow; spurred petal 10–15 mm. long, the saccate spur 3–4 mm. long, blunt, the very short hood not crested, the wing margin minute but relatively broad, folded back upon the hood; spurless outer petal 10–13 mm. long; inner petals 9–12 mm. long, the slender claw 6–8 mm. long, occupying about two-thirds of the total length, the blade obovate, much broader near the apex, having a very high, angular, medial fold; stamen spur blunt, 1 mm. or less long, one-third the length of the petal spur; stigma slightly broader apically, with 4 papillary stigmatic surfaces; fruits erect, the slender body 25–50 (usually 30–35) mm. long, straight or somewhat curved, many-seeded; seeds about 1 mm. in diameter, black, shiny, turgid, distinctly decorated under magnification, the margin obtuse.

C. sempervirens is recognized easily by its erect habit, its divaricately branched stems, its pink and yellow flowers, its very slender, erect or spreading fruits, and numerous minute, decorated seeds. It has no close relatives in America.

This widely distributed species has no discernible geographical variants. Two

local variants, however, have been observed. Plants collected by Bartlett at Medford, Mass., have exceptionally stout, incurved fruits, and a collection made by Ehlers at Prentis Bay, Michigan, has unusually small flowers. It is doubtful if either of these variants is of nomenclatorial consequence.

In shallow, often dry soil, rock ledges, crevices, and talus, and on burned or otherwise disturbed areas, at elevations of about 500–5000 feet; northeastern Georgia to Maine and Newfoundland, thence westward to Montana and British Columbia and northwestward to Alaska. Flowers throughout the summer months from about May 15 to September 15; fruits from about June 1 to September 30.



Map 4. Distribution of *Corydalis sempervirens* (L.) Pers.

GEORGIA: Rabun County.

SOUTH CAROLINA: Pickens County.

NORTH CAROLINA: Alexander, Buncombe, Burke, Caldwell, Forsythe, Haywood, Henderson, Jackson, Macon, Mitchell, Transylvania, Watauga, and Wilkes counties.

TENNESSEE: Carter County.

KENTUCKY: Bell and Harland counties.

VIRGINIA: Augusta, Bedford, Carroll, Giles, Lee, Madison, Loudoun, Page, Pulaski, Rappahannock, Rockingham, Shenandoah, and Smythe counties; Shenandoah National Park.

WEST VIRGINIA: Grant, Mineral, Monroe, Pocahontas, Preston, Raleigh, and Webster counties.

MARYLAND: Allegany, Frederick, and Garrett counties.

PENNSYLVANIA: Adams, Bedford, Bucks, Elk, Fayette, Indiana, Lancaster, Luzerne, Lycoming, Monroe, Montgomery, Northampton, Perry, Philadelphia, Union, Westmoreland, and York counties.

NEW JERSEY: Bergen, Essex, Hunterdon, Ocean, Passaic, Sussex, and Warren counties.

NEW YORK: Albany, Dutchess, Essex, Franklin, Greene, Herkimer, Jefferson, Nassau, Orange, Putnam, Rensselaer, St. Lawrence, Saratoga, Tompkins, Warren, Washington, and Westchester counties.

CONNECTICUT: Fairfield, Hartford, Middlesex, New Haven, and New London counties.

RHODE ISLAND: Providence County.

MASSACHUSETTS: Berkshire, Essex, Franklin, Hampden, Hampshire, Middlesex, Norfolk, Suffolk, and Worcester counties.

VERMONT: Addison, Caledonia, Chittenden, Orange, Rutland, and Windham counties.

NEW HAMPSHIRE: Carroll, Cheshire, Coos, Grafton, and Hillsboro counties.

MAINE: Aroostook, Cumberland, Franklin, Hancock, Knox, Lincoln, Oxford, Penobscot, Sagadahoc, Somerset, Washington, and York counties.

OHIO: Lake and Portage counties.

INDIANA: Lake and Starke counties.

ILLINOIS: Cook, LaSalle, and Ogle counties.

MICHIGAN: Cheboygan, Crawford, Emmet, Ingham, Keweenaw, Leelanau, Mackinac, Marquette, Muskegon, and St. Clair counties.

WISCONSIN: Adams, Ashland, Bayfield, Brown, Oneida, Polk, Sauk, Sawyer, Shawano, and Vilas counties.

MINNESOTA: Aitkin, Beltrami, Carlton, Cass, Chisago, Clearwater, Cook, Itasca, Lake, Millelacs, and St. Louis counties.

MONTANA: Flathead County; Glacier National Park.

NEWFOUNDLAND: gravelly railroad embankments, Grand Falls, July 4, 1911, *Fernald & Wiegand 5455* (NY, G); sandy terraces, n. bank of river above the falls, Bishop's Falls, valley of Exploits River, July 28 & 29, 1911, *Fernald & Wiegand 5456* (G); dry woods, Buchan (?) Junction, July 13, 1930, *Jaussan* (G); railway, Gambo, July 14, 1893, *Waghorne 21* (UA).

NOVA SCOTIA: DIGBY CO.—clearing at border of deciduous woods, Wentworth Lake, Sept. 4, 1921, *Fernald & Long 23866* (G). INVERNESS CO.—dripping cliffs, Big Intervale, July 17, 1941, *Roland 41416* (G). LUNENBURG CO.—recently burned clearing w. of Bridgewater, Aug. 18, 1921, *Fernald & Long 23865* (G).

PRINCE EDWARD ISLAND: PRINCE CO.—dry clearings, Alberton, July 11, 1912, *Fernald & St. John 7502* (WS, NY, G, US).

NEW BRUNSWICK: KENT CO.—Bass River, June 10, 1869, *Fowler* (G).

QUEBEC: BROME CO.—Mt. Elephantis, Brome, July 30, 1902, *Pease 606* (G); dry mountain ledge, Bolton, July 25, 1926, *Knowlton* (G). CHAMBLY CO.—St. Hubert: Tourbieres, environs de Montreal, June, 1913, *Victorin 206* (M, WS, US). CHARLEVOIX CO.—vicinity of Cap à L'Aigle, July 27, 1905, *Macoun* (G). GASPÉ CO.—alluvial woods, York River, July 29, 1905, *Williams, Collins & Fernald* (G). KAMOURASKA CO.—dry, quartzite hills, Ste. Anne, July 14, 1922, *Fernald & Pease 25088* (G). LAKE ST. JOHN DIST.—carrière de granit, Roberval, July 20, 1921, *Victorin 15757* (G). MEGANTIC CO.—dry, serpentine slopes and crests of Caribou Hill, Black Lake, Aug. 26, 1915, *Fernald & Jackson 12098* (G). NISSISQUOI CO.—rocky places, Philipsburg, June 22, 1910, *Edmondson 4995* (G). MONTMAGNY CO.—Grosse-Ile, l'estuaire du Saint-Laurent, July 31, 1935, *Victorin, Rolland-Germain, Rousseau & Meilleur 40082* (G). PONTIAC CO.—Ile-des-Soeurs, Lake Timiscaming, June 26, 1918, *Victorin 8365* (US). RICHMOND CO.—dry ledge, Cleveland, July 30, 1923, *Chamberlain & Knowlton* (M, G). RIMOUSKI CO.—dans un champ près du chemin du cap à l'Orignal, Aug. 19, 1927, *Rousseau 26971* (CIUC). TERREBONNE CO.—sur les gneiss laurentiens, St. Jerome, July 4, 1930, *Victorin & Rolland-Germain 33122* (RM, G). TWO MTS. CO.—La Trappe, Oct. 9, 1926, *Louis-Marie* (G). CO. UNCERTAIN—on rocks along Matamek River, n. shore, July 26, 1927, *Bowman 247* (G); Lac Kamatose, sur le ballast de la route, 101 milles au nord de Mont-Laurier, Aug. 23–25, 1941, *Victorin, Rolland-Germain & Dominique 260* (G).

ONTARIO: ALGONA DIST.—thin soil, e. ridge, Havilland Bay, 47° 00′ N., 84° 45′ W., Aug. 12, 1935, *Taylor, Hosie, Fitzpatrick, Losee & Leslie 1310* (US). CARLETON CO.—Cascades, vicinity of Ottawa, July 31, 1920, *Victorin 10055* (WS). FRONTENAC CO.—

Battersea, June 13, 1898, *Edmondson 1106* (NY); Kingston, May 30, 1901, *Fowler* (G, US); Barriefield, June, 1897, *Boyd* (M). KENORA DIST.—Minaki, July 25, 1915, *Thompson 30* (M). LEEDS CO.—Jones Falls, June 7, 1895, *Fowler* (US). MUSKOKA DIST.—crevices of rocks, Lake Joseph, Muskoka, Aug. 20, 1881, *Burgess* (M); Lake Muskoka, Aug. 16–18, 1898, *Topping* (US). NIPISSING DIST.—common on sunny rocks, Twin Islands, Timagami region, July 24, 1926, *Anderson & Anderson 26039* (M, NY, G); Cache Lake, Algonquin Park, July 4, 1900, *Macoun* (US); open, grassy woods, Sturgeon Falls near Lake Nipissing, Aug. 14, 1937, *Nelson & Nelson 2395* (RM). PARRY SOUND DIST.—Island 74 in French River, July 5, 1939, *Dewey 1* (US); in soil pockets on granite ridge, s. side of French River Harbor, n. w. part of Parry Sound, Sept. 6, 1932, *Grassl 3766* (NY). RENFREW CO.—bluffs, Bonne Chere Mts., July 20, 1899, *Umbach* (US). THUNDER BAY DIST.—Mungo Park Point, Nipigon Lake, 1912, *Pulling* (G); crevice of altered lava, rocky knoll, flat e. of Schreiber, Aug. 21, 1937, *Hosie, Losee & Bannan 1412* (G); dry ledges, S. Slate Island, July 6, 1933, *Pease & Bean 23,540* (G); black loam along Amadis River, 1912, *Pulling* (G); diabase crevices, Shangoina Island, Sibley Tp., 48° 20′ N., 88° 50′ W., July 6, 1936, *Taylor, Losee & Bannan 505* (D). TIMISKAMING DIST.—Moose River Basin, 1903, *Bell* (G).

MANITOBA: SELKIRK DIST.—Elk Island, Lake Winnipeg, July 20, 1887, *Macoun* (NY). DIST. UNCERTAIN—Piguitonay (mile 214), route of Hudson Bay Railway, July 8, 1917, *Emerton* (G); Lake Winnipeg Valley, 1857, *Bourgeau* (G).

SASKATCHEWAN: north shore, Athabaska Lake, July 26, 1920, *Laing 174* (US); exposed rocky slopes, Charlot Pt., Lake Athabaska, about 59° 36′ N., 109° 13′ W., June 12, 1935, *Raup 6088* (G); in clay and sandy soil, Sulphide Lake (Lac la Ronge), Oct. 3, 1941, *Studer 4–16* (CIUC).

ALBERTA: ATHABASKA DIST.—Egg Lake, Athabaska Delta, July 18, 1920, *Harper 53* (US); Smith Landing, June 13, 1903, *Preble & Cary 13* (US); Granite Hill, Gov. Hay Camp district, Slave River, about 59° 31′ N., 11° 28′ W., Wood Buffalo Park, Mackenzie Basin, Aug. 14, 15, 1928, *Raup 2443-a* (G); short distance e. of Sand Point, n. shore of Lake Athabaska, about 58° 57′ N., 110° 42′ W., 700 ft. alt., Sept. 1, 1932, *Raup & Abbe 4531*. PEACE RIVER DIST.—Notikewin, Peace River region, roadside in poplar woods, 57° N., 118° W., July 12, 1931, *Moss 2255* (WS).

BRITISH COLUMBIA: CARIBOO DIST.—Hargreaves Ranch, 2900 ft. alt., Mt. Robson, Aug. 19–26, 1943, *Scamman 3272* (G, US); in brush on rocky slope, Campbell Island in Summit Lake, 31 mi. n. of Prince George, Aug. 1, 1941, *Weber 2600* (WS, M, NY, G, US). COAST DIST.—Bute Inlet, without date, *Anderson* (WS). KOOTENAY DIST.—Revelstoke, May 27, 1890, *Macoun* (US); deserted log road, Revelstoke, July 6, 1905, *Shaw 830* (NY, G, US). NEW WESTMINSTER DIST.—Cheak Kamis, June 25, 1920, ex herb. *Anderson* (WS); Mons, P. G. E. Railway, June 20, 1916, *Macoun* (NY, G).

YUKON: n. side of Moose Creek near Clark's Peak, 3500 ft. alt., Mayo District between Stewart and MacMillan Rivers, Aug. 7, 1939, *Bostock 60* (G); Klondyke, Aug. 23, 1898–1901, *MacLean* (UC, G); Moosehide Mt., Dawson, July 14, 1902, *Macoun* (NY); Bonanza Creek, Aug. 11, 1899, *Tarleton 178a* (NY); Dawson, July 17, 1898, *Williams* (NY).

ALASKA: edge of airfield, Franklin, Fortymile dist., July 16, 1941, *Anderson & Gasser 7320* (RM, G); dry ground, The Birches, 55 mi. below Tanana, on the Yukon River, July 8, 1902, *Brooks* (G); roadside near Knik, Oct., 1913, *Chaney 151* (M); Eagle to Valdes trail, June 30, 1902, *Collier 72* (US); headquarters, Mt. McKinley Nat. Park, June 28, 1932, *Dixon 45* (UC); Hot Springs on the Tanana River, July 28, 29, 1909, *Hitchcock* (US); Rampart, July 26, 1901, *Jones 67* (US); Mt. McKinley Nat. Park, summer, 1932, *Kaye 1501* (UC); Dall River Trail, 3 mi. above Dall City, Ft. Hamlin, Yukon River, to Bergman, Koyukuk River, June 29, 1901, *Mendenhall* (US); n. of superintendent's office, 3000 ft. alt., Mt. McKinley Nat. Park, July 23, 1928, *Mexia 2106* (M, UC, D, NY, G, US); exposed hillsides above spruce woods, e. side of Wonder Lake, near center of n. boundary of Mt. McKinley Nat. Park, Aug. 14, 1928, *Mexia 2240* (M, UC, D, NY, G, US); McKinley Park Station, July 31, 1922, *Murie* (US); rocky soil near Park Headquarters, Mt. McKinley Nat. Park, June 22, 1939, *Nelson & Nelson W-2151*

(RM); open woods just below Park Headquarters, Mt. McKinley Nat. Park, July 3, 1939, *Nelson & Nelson 3622* (RM, G); roadside near Park Headquarters, Mt. McKinley Nat. Park, July 16, 1939, *Nelson & Nelson 3833* (M, RM, IH, NY, G); Fairbanks, June, 1927, *Palmer 1769* (US); recent clearings and open woods, Goldstream Creek and Pedro Dome, 51 mi. n. of Fairbanks, 65° N., 147° 30′ W., 800–2000 ft. alt., June 13, 1926, *Porsild & Porsild 135* (G); open, forested bottom lands, Kokrines Mts., n. side of divide, towards Melozitna River, 65° 20′ N., 154° 30′ W., 800–4000 ft. alt., June 23–July 5, 1926, *Porsild & Porsild 739* (G); hill s. of Mitchell Creek, 3000 ft. alt., Copper River region, Aug. 6, 1902, *Poto 121* (US); Anchorage area, May 23, 1943, *York 4* (M); sandy hillside near Palmer, July 5, 1943, *York Pa208* (M); Mt. McKinley Nat. Park, 63° 43′ N., 149° 15′ W., July 5–7, 1936, *Scamman 213* (G); Livengood, about 80 mi. n.-n.w. of Fairbanks, June 19–21, 1940, *Scamman 1735* (CIUC, G); Gens de Large (Chandler River) & Koyukuk rivers, 1899, *Schrader* (US).

5. C. FLAVULA (Raf.) DC. Prod. Syst. Nat. **1**:129. 1824.

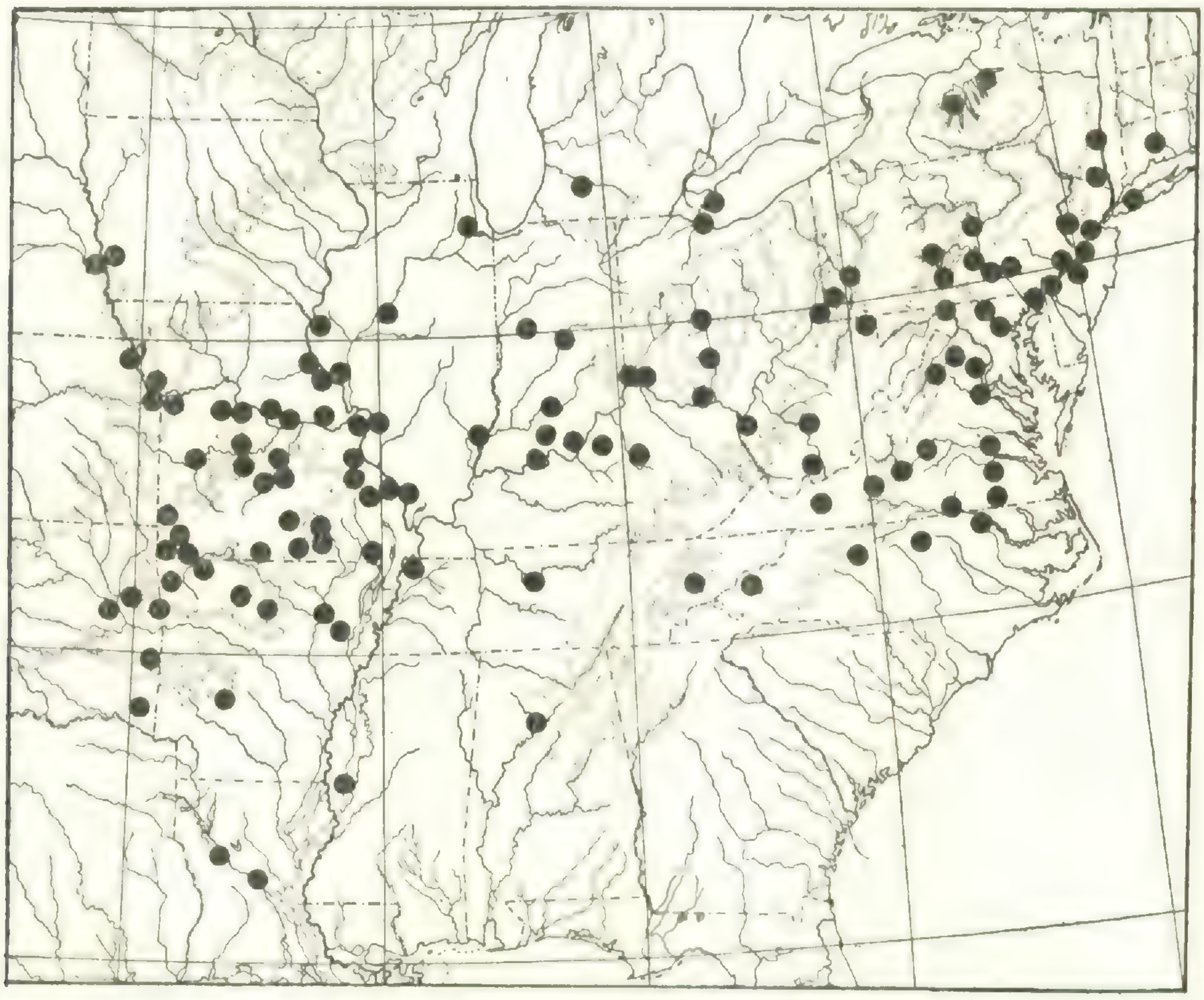
Fumaria flavula Raf. in Desv. Jour. Bot. **1**:224. 1808.
Corydalis aurea α *flavula* Wood, Am. Bot. & Fl. 34. 1870.
Corydalis flavidula Chapm. Fl. S. U. S. Suppl. **1**:604. 1883, sphalm.
Capnodes flavulum Ktze. Rev. Gen. **1**:14. 1891.
Neckeria flavula Millsp. Fl. W. Va. 327. 1892 (W. Va. Agr. Exp. Sta. Bull. 2).
Corydalis Geyeri Fedde, Rep. Spec. Nov. **10**:311. 1912.

Green or glaucous winter annual; stems 1–several, sympodial, commonly 15–30 cm. tall, erect while young, often prostrate or ascending when older; basal leaves long-petioled; cauline leaves short-petioled to almost sessile, hardly reduced in size upward; leaf blades pinnate, with 5–7 segments which are again pinnatifid into about 5 lobes, these again incised; ultimate leaf segments narrowly to broadly elliptical, subapiculate, varying greatly in size; racemes equalling or barely exceeding the leaves, commonly 6- to 10- or more flowered, sometimes poorly developed; cleistogamous-flowered racemes, when present, inconspicuous, 1- to 5-flowered; floral bracts broadly to narrowly elliptical, 6–12 mm. long, 3–7 mm. broad, the lowermost often foliose or variously incised, becoming entire and reduced upward; pedicels slender, erect at anthesis, reflexed in fruit, 6–15 mm. or more long; sepals scarious, fugacious, about 1 mm. long, lanceolate; flowers pale yellow, somewhat crowded; spurred petal 7–9 mm. long, the hood crested, the crest high, undulate or toothed, the wing margin well developed, also undulate or toothed, the incurved spur about 2 mm. long; spurless outer petal 6–8 mm. long, the crest and wing margin as in the spurred petal; clawed inner petals 5–7 mm. long, the claw 2–3 mm. long, the blade approximately twice as broad near the apex as at the distinctly lobed base; stamen spur less than 1 mm. long, less than one-half the length of the petal spur; stigma broader than high; fruits reflexed or variously disposed, 14–22 (often 18–20) mm. long, straight, essentially glabrous; seeds about 2 mm. in diameter, black, shiny, on magnification seen to be concentrically, submuricately decorated on the narrow, acute ring margin.

This species is easily distinguished by the small, crested flowers, the very short, incurved spur, and long, reflexed pedicels. Cleistogamous-flowered plants are col-

lected occasionally, and these often have much broader and larger ultimate leaf segments and weaker, more diffusely branched stems. Such plants can be determined accurately by fruit characters alone.

Moist, loose soil, wooded slopes and bottom lands, at elevations up to about 2000 feet; Connecticut and New York to North Carolina westward to northern Louisiana, eastern Oklahoma, Kansas and Nebraska. Flowers in early spring from about March 15 to May 15; fruits from about April 1 to June 1.



Map 5. Distribution of *Corydalis flavula* (Raf.) DC.

Connecticut: Middlesex County.
New York: Nassau, Onondaga, Rockland, Ulster, and Yates counties.
New Jersey: Camden, Hunterdon, Mercer, and Somerset counties.
Pennsylvania: Allegheny, Franklin, Huntingdon, Lancaster, Montgomery, Perry, Philadelphia, Snyder, Washington, and York counties.
Delaware: Newcastle County.
Maryland: Allegany, Baltimore, Carroll, Cecil, Hartford, Howard, Montgomery, and Prince Georges counties.
Virginia: Albemarle, Alexandria, Bedford, Botetourt, Buckingham, Dinwiddie, Fairfax, Fauquier, Greenesville, Henrico, Mecklenburg, Prince George, Prince William, Pulaski, Roanoke, Shenandoah, Stafford, Warren, and Wythe counties.
West Virginia: Berkeley, Cabell, Fayette, Monongalia, Ohio, and Raleigh counties.
North Carolina: Durham, Forsythe, Halifax, and Madison counties.
Kentucky: Fayette, Shelby, and Woodford counties.
Tennessee: Blount, Davidson, Knox, and Obion counties.

ALABAMA: Tuscaloosa County.
MISSISSIPPI: Sharkey County.
LOUISIANA: Natchitoches and Rapides parishes.
ONTARIO: Essex County, Point Pelee and Pelee Island.
MICHIGAN: Kalamazoo County.
OHIO: Clermont, Franklin, Hamilton, Ottawa, Ross, Scioto, and Warren counties.
INDIANA: Floyd, Lawrence, Marion, Montgomery, Orange, and Perry counties.
ILLINOIS: Hancock, Jackson, Mason, Pike, St. Clair, Union, Wabash, and Will counties.
MISSOURI: Barry, Boone, Butler, Callaway, Camden, Clay, Cooper, Franklin, Howell, Jackson, Jasper, Jefferson, Lawrence, McDonald, Madison, Maries, Marion, Montgomery, Morgan, Oregon, Ozark, Perry, Pettis, Phelps, Pulaski, St. Clair, St. Francois, Ste. Genevieve, St. Louis, Shannon, Texas, Warren, and Washington counties.
IOWA: Pottawattomie County.
NEBRASKA: Sarpy County.
KANSAS: Atchinson and Wyandotte counties.
OKLAHOMA: Adair, Cherokee, LeFlore, McCurtain, and Muskogee counties.
ARKANSAS: Carroll, Cross, Garland, Jackson, Searcy, Van Buren, and Washington counties.

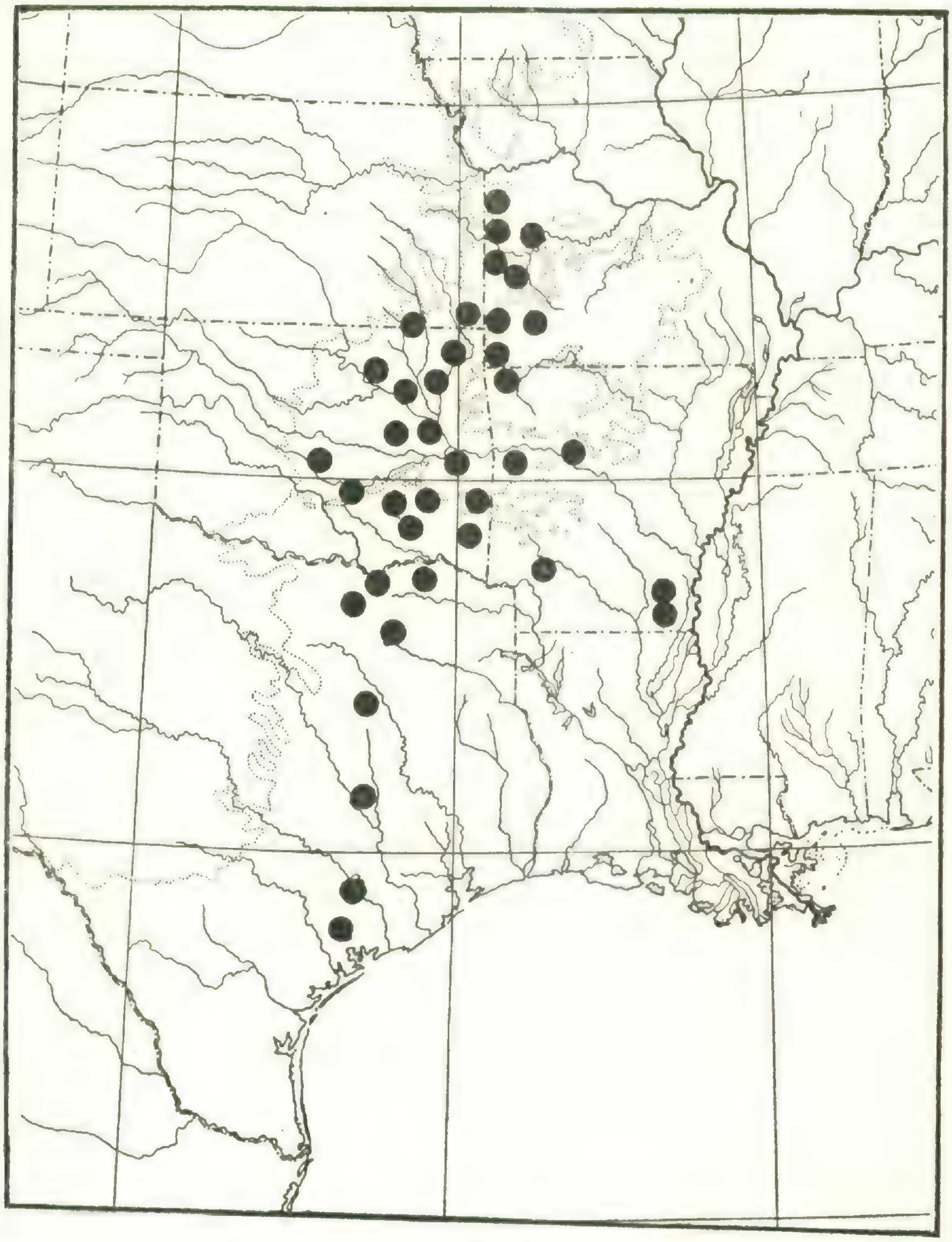
6. C. CRYSTALLINA Engelm. apud Gray, Man. Bot. ed. 5. 62. 1867; Bot. Gaz. **11**:189. 1886.

Corydalis aurea β. *? crystallina* Torr. & Gray, Fl. N. Am. **1**:665. 1840.
Corydalis crystallina Engelm. ex Torr. & Gray, l. c. 1840, as syn.
Capnodes crystallinum Ktze. Rev. Gen. **1**:14. 1891.
Capnoides Halei Small, in Bull. Torr. Bot. Club **25**:137. 1898, as to most of Hale's collection from Louisiana.
Corydallis crystallina var. *strictissima* Fedde, Rep. Spec. Nov. **10**:479. 1912.

Glaucous winter annual; stems 1–several, often sympodial, 20–40 cm. tall, erect or ascending; basal leaves long-petioled; cauline leaves short-petioled to sessile, somewhat reduced upward; leaf blades pinnate, the segments pinnatifid and once again incised, the ultimate lobes broadly lanceolate to linear-lanceolate, subapiculate; primary racemes surpassing the leaves, 8- to 18- (ordinarily 12- to 15-) flowered, the later secondary racemes fewer-flowered; bracts ovate to ovate-acuminate, 5–12 mm. long, 3–6 mm. broad, usually much reduced upward; pedicels stout, erect, about 1 mm. long; sepals scarious, fugacious, 2 mm. or less long, broadly ovate to cordate, somewhat attenuate, the margin sometimes incised, especially at the base; flowers bright yellow, crowded at first, becoming more distant at anthesis; spurred petal 16–22 mm. long, the hood always crested, the crest very high, undulate or toothed, the wing margin very broad, reflexed upon the hood, the spur 6–8 mm. long, the blunt tip distinctly globose; spurless outer petal 12–14 mm. long, about 3 mm. longer than the inner petals, the wing margin wide, not reflexed upon the hood, enclosing the margins of the spurred petal in the bud, the crest as in the spurred petal; inner petals oblanceolate, 9–11 mm. long, the narrow claw 4–5 mm. long, the blade about twice as wide at the tip as at the base, the basal lobes small; stamen spur 3.5–5.0 mm. long, clavate, curved or bent near the apex; stigma about twice as broad as high; style long and slender; fruits erect, 14–18 mm. long, stout, straight or moderately incurved toward the floral axis, densely beset with transparent, clavate pustules which often break open at

maturity or, rarely, glabrate; seeds black, about 2 mm. in diameter, distinctly submuricately decorated under magnification, having no ring margin.

This species is distinguished from all other species of *Corydalis* by the peculiar type of pubescence of the fruit. The pustules sometimes appear ligulate when desiccated or, as is often the case, when they rupture at maturity. The crest and margins of the hood of the outer petals are more highly developed than in any other yellow-flowered species.



Map 6. Distribution of *Corydalis crystallina* Engelm.

C. crystallina var. *strictissima* is a habitat variant and of no systematic value. The type was collected by F. L. Harvey in "Orchards, grain fields, etc., Northwest Arkansas," and was distributed as Curtiss's North American Plants *125**. Fedde cites the collection but gives the number erroneously as *125a*. Too, he previously had described *C. micrantha* var. *diffusa*, a synonym of *C. micrantha* ssp. *australis*, on the basis of the true Curtiss's North American Plants distribution *#125a*, collected by Curtiss himself in Duval County, Florida.

Prairies, fields, open woods, and wasteland; southwestern Missouri to central Texas. Flowers in early spring from about April 1 to May 15; fruits from about April 15 to June 1.

MISSOURI: Bates, Benton, Cass, Greene, Henry, Jasper, Lawrence, McDonald, Newton, St. Clair, and Vernon counties.

ARKANSAS: Ashley, Benton, Carroll, Drew, Franklin, Nevada, Pope, Sebastian, and Washington counties.

KANSAS: Cherokee and Montgomery counties.

OKLAHOMA: Atoka, Cleveland, Craig, Haskell, Latimer, LeFlore, McCurtain, Mayes, Muskogee, Okmulgee, Osage, Pittsburg, Pontotoc, Pushmataha, Rogers, and Tulsa counties.

TEXAS: Brazos, Colorado, Denton, Fannin, Grayson, Kaufman, Lamar, Navarro, Tarrant, Van Zandt, and Victoria counties.

7. C. MICRANTHA (Engelm.) Gray ssp. **micrantha** G. B. Ownbey, stat. nov.

Corydalis aurea var. *micrantha* Engelm. apud Gray, Man. Bot. ed. 5. 62. 1867.
Corydalis micrantha Gray, in Bot. Gaz. **11**:189. 1886, in part.
Neckeria micrantha MacMillan, Metasp. Minn. Valley. 255. 1892.
Capnoides micranthum Britton, in Mem. Torr. Bot. Club **5**:166. 1894.
Corydalis micrantha var. *pachysiliquosa* Fedde, Rep. Spec. Nov. **10**:380. 1912.
Corydalis monilifera var. *ferruginifera* Fedde, l. c. **11**:498. 1913.

Glaucous or nearly green winter annual; stems 1–several, usually 15–25 cm. tall, erect or ascending, sparingly branched; basal leaves crowded, long-petioled; cauline leaves short-petioled to nearly sessile, gradually reduced upward; leaf blades pinnate, the 5–7 primary segments pinnatifid and again incised, the ultimate lobes oblong-elliptical or obovate, subapiculate; normal-flowered racemes usually present, slightly exceeding the leaves, 6- to 16-flowered, not surpassed by the fewer-flowered secondary racemes; cleistogamous-flowered racemes, when present, inconspicuous, 1- to 5-flowered; bracts elliptical, the lowermost 5–8 mm. long and 2–4 mm. broad, the upper much reduced, often minute on cleistogamous-flowered racemes; pedicels erect, the lower usually 2–4 mm. long, gradually decreasing in length upward; sepals scarious, fugacious, 1.5 mm. or less long, ovate, often undulate or toothed at the margin; flowers pale yellow, often somewhat crowded throughout anthesis; spurred petal 11–15, usually 12–14 mm. long, the hood crested, the crest low, undulate or rarely obsolescent, the wing margin well developed, the spur 4.5–6.0 mm. long, the apex distinctly globose; spurless outer petal 9–11 mm. long, semi-geniculate, the crest low; inner petals 7–9 mm. long, oblanceolate, the claw 3–4 mm. long, the blade twice as broad at the apex as at the obscurely lobed base; stamen spur 3–4 mm. long, about three-fifths the length of

the petal spur, straight or curved, sometimes clavate; stigma 2-lobed, rectangular, twice as wide as high; fruits erect, commonly 10–15 mm. long, rarely longer, often shorter in cleistogamous-flowered racemes, straight or moderately incurved; seeds about 1.5 mm. in diameter, black, shiny, turgid, concentrically but moderately decorated under magnification, obtuse at the border, with no ring margin.

The subspecies of *C. micrantha* are all characterized by very small seeds and can be distinguished from all other yellow-flowered species by them alone. Subspecies *micrantha* usually can be distinguished from ssp. *australis* by its less elongated racemes, generally smaller flowers, globose tipped spur and generally shorter, stouter fruits. The two subspecies intergrade in all of these characters, especially in southern Missouri and Oklahoma, but in most cases the disposition of a given specimen is not difficult. In southern Missouri a form is also found which is characterized by larger, more showy flowers, longer pedicels, and relatively short fruits. This large-flowered form has been confused by various authors with *C. aurea*. As flower size is not considered a good criterion for separation of the segregates of *C. micrantha*, this form seems better left with the typical subspecies.

A dwarf form of ssp. *micrantha* was collected by Reverchon at Columbia, Brazoria Co., Texas. This locality is far removed from the expected range of the subspecies and it seems likely that data on the label are mixed. Its presence there should be verified.

Although encountered occasionally in other species of *Corydalis* the cleistogamous condition reaches its highest development in *C. micrantha*. It occurs at random throughout the range of the species. A single plant may have only normal flowers, only cleistogamous flowers, or both cleistogamous and normal flowers. In the last instance, the cleistogamous flowers are produced only on the smaller, less well-developed secondary branches. Plants having only cleistogamous flowers are quite different in aspect, usually being much more profusely and delicately branched. The racemes are short, weak, and ordinarily have 1–5 small, undeveloped, self-fertilized flowers and ultimately the same number of fruits crowded near the apex. The disposition of such specimens is likely to prove difficult for one who is unfamiliar with this type of variation.

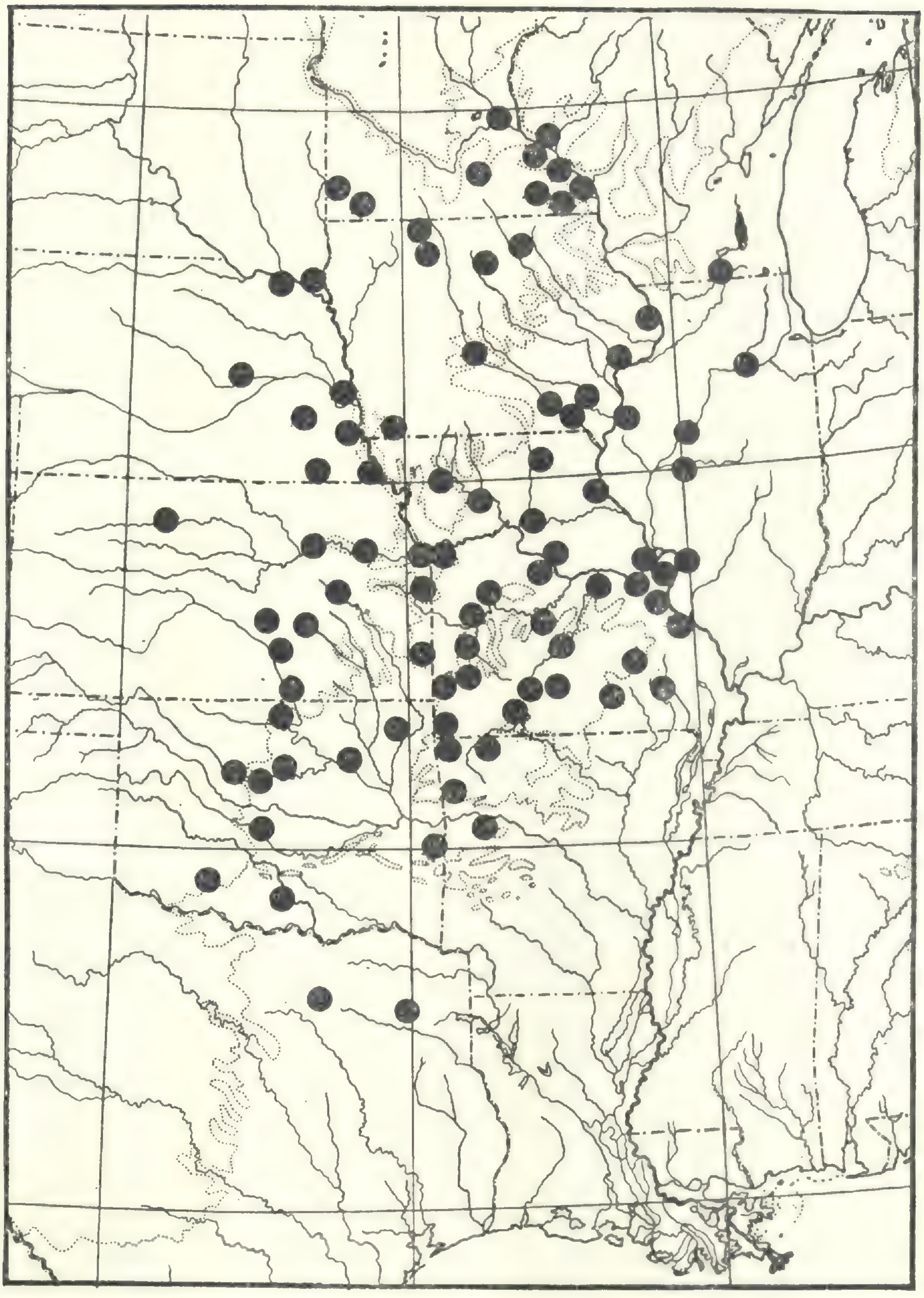
The conditions which institute cleistogamy are not entirely understood. It is notable, however, that plants growing in the shade or those which are crowded together so that they shade each other are predominantly cleistogamous. Also, age of the plant is of some significance, as the later racemes are often entirely cleistogamous on plants which at first produced only normal flowers.

Along bluffs, rocky hills, open woods, and river banks, often in disturbed soil; southern Minnesota to Illinois, Kansas, and northern Texas. Flowers in early spring from about April 1 to May 15; fruits from about April 15 to June 1.

MINNESOTA: Fillmore, Goodhue, Hennepin, Murray, Nobles, Olmsted, Pipestone, Steele, and Winona counties.

WISCONSIN: Pepin and Rock counties.

IOWA: Dickinson, Emmet, Floyd, Henry, Jackson, Muscatine, Page, Palo Alto, Polk, Van Buren, Wapello, and Wright counties.



Map 7. Distribution of *Corydalis micrantha* (Engelm.) Gray ssp. *micrantha* Ownbey.

ILLINOIS: Henderson, LaSalle, Menard, Peoria, and St. Clair counties.

MISSOURI: Adair, Boone, Camden, Cass, Cedar, Christian, Dade, Daviess, Gasconade, Greene, Henry, Iron, Jackson, Jasper, Jefferson, Lawrence, Livingston, McDonald, Marion, Miller, Moniteau, Phelps, Polk, Pulaski, Ralls, Randolph, St. Charles, St. Clair, Ste. Genevieve, St. Louis, Shannon, Stone, Texas, Wayne, and Webster counties.

ARKANSAS: Benton, Carroll, Logan, and Washington counties.

SOUTH DAKOTA: Clay County.

NEBRASKA: Cass, Cedar, Gage, Lancaster, Nance, Otoe, Richardson, and Sarpy counties.

KANSAS: Bourbon, Chase, Cowley, Geary, Harvey, Lyon, Miami, Osborne, Riley, Sedgwick, Shawnee, and Wyandotte counties.

OKLAHOMA: Carter, Comanche, Kay, Kingfisher, LeFlore, Logan, McClain, Murray, Oklahoma, Payne, Rogers, and Tulsa counties.

TEXAS: Brazoria, Dallas, and Upshur counties.

7a. C. MICRANTHA (Engelm.) Gray ssp. **australis** (Chapm.) G. B. Ownbey, stat. nov.

Corydalis aurea var. *australis* Chapm. Fl. S. U. S. Suppl. 1:604. 1883.
Corydalis micrantha Gray, in Bot. Gaz. 11:189. 1886, in part.
Capnoides Halei Small, in Bull. Torr. Bot. Club 25:137. 1898, as to the Curtiss collections from Jacksonville, Florida, but not as to most of Hale's specimens from Louisiana.
Capnoides campestre Britton, Man. ed. 2. 1065. 1905.
Corydalis curvisiliqua var. *tenerior* Fedde, Rep. Spec. Nov. 10:365. 1912.
Corydalis micrantha var. *diffusa* Fedde, l. c. 380. 1912.
Corydalis micrantha var. *leptosiliqua* Fedde, l. c. 11:497. 1913.
Corydalis campestris Buchholz & Palmer, in Trans. Acad. Sci. St. Louis 25:115. 1926.
Corydalis Halei Fernald & Schubert, in Rhodora 48:207. 1946.

Green or somewhat glaucous annual; stems 1–several, usually 20–40, occasionally up to 60 cm. tall, the earlier usually stouter, semi-erect, the later ascending; basal leaves crowded, long-petioled; cauline leaves short-petioled or nearly sessile, reduced upward; leaf blades pinnate, the 5–7 primary segments pinnatifid and again incised, the ultimate lobes longer than broad, approximately ovate, subapiculate; normal-flowered racemes usually present, much surpassing the leaves, 10- to 20-flowered, not surpassed by secondary racemes; cleistogamous-flowered racemes, when present, inconspicuous, 1- to 5-flowered; bracts elliptical, usually less than 8 mm. long and 4 mm. broad, the upper much reduced; pedicels erect, the lower 3–6 mm. long, decreasing in length upward; sepals scarious, fugacious, 1.5 mm. or less long, broadly ovate, the margin undulate or toothed especially at the base; flowers pale yellow, becoming distant during anthesis; spurred petal 12–14 mm. long, the hood nearly always crested, the crest low, regular or undulate, the wing margin well developed, the spur 4–6 mm. long, the tip blunt, never distinctly globose; spurless outer petal 9–11 mm. long, geniculate, the crest low; inner petals 8–10 mm. long, oblanceolate, the claw 3–4 mm. long, the blade twice as broad near the apex as at the obscurely lobed base; stamen spur 2.5–3.5 mm. long, about three-fifths the length of the petal spur, usually straight, sometimes bent near the tip, clavate; stigma 2-lobed, rectangular, twice as wide as high; fruits erect, 15–20, rarely 25 mm. long, slender, straight or moderately incurved; seeds

about 1.5 mm. in diameter, black, shiny, concentrically but moderately decorated under magnification, obtuse at the border, with no ring margin.

Subspecies *australis* is best distinguished by its elongate normal-flowered racemes, its short, saccate spur which is never clearly globose at the tip, its slender, erect fruits, and its minute, nearly smooth seeds.

The peculiarities of this plant were first recognized by Chapman who in 1883 published a short and accurate description of it in the first supplement to his 'Flora' under the name *Corydalis aurea* var. *australis*. In 1886 Gray (Bot. Gaz. **11**:189), in his study of *C. aurea* and its allies, concluded that Chapman's variety belonged with *C. micrantha* and reduced it to synonymy under that species. In conformance with Gray's treatment Chapman, then, also treated his variety as a synonym of *C. micrantha* in the third edition of his 'Flora' issued in 1897. The following year Small redescribed Chapman's plant as *Capnoides Halei*.

Small's description of *Capnoides Halei* was drawn on the joint basis of Hale's collection from Louisiana and Curtiss's collections from Florida. Hale's plants (s. n. in Herb. N. Y. Bot. Gard.), are all *C. crystallina* except for one small specimen which is referable to the subspecies described above. It is evident from the general aspect of the plants of *C. crystallina* that they are those referred to by Small in comparing the "new" species with *Capnoides curvisiliquum (Corydalis curvisiliqua)* when he distinguished it from that species by ". . . . its more slender habit, and especially by the more coarsely dissected leaf-blades."

Also cited by Small was *Curtiss 4515* from Jacksonville, Florida, and with the exception of the sentence quoted above, it is from these Florida specimens that the description is drawn. They, therefore, should be designated the authentic type if the species were maintained.

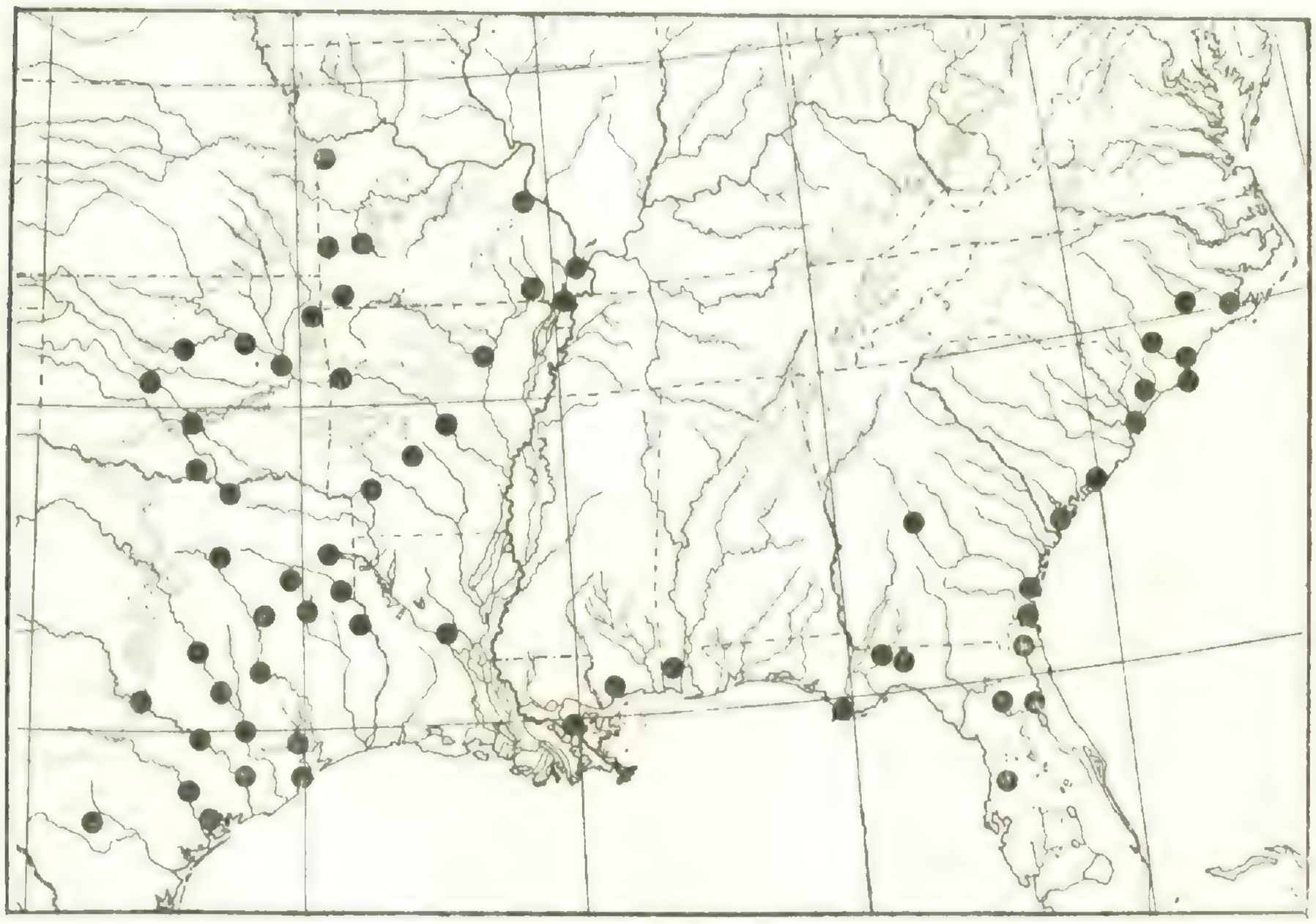
This entity has been the subject of a recent paper by Fernald and Schubert (Rhodora 48:207. 1946) who, recognizing its distinctness, have revived Small's name, and transferred it to *Corydalis*. I do not believe, however, that the differences between this and ssp. *micrantha* are of specific level, and am therefore taking up Chapman's earlier varietal name *australis* in its new rank of subspecies. In support of this view it may be mentioned that seeds of ssp. *micrantha* and ssp. *australis* are identical in size and decoration of the testa, that the flowers are similar in that both have a low crest, and that the geographical distrubution of the two subspecies taken as a whole is not unnatural. Even greater variability in habit, together with similar minor morphological variability of the floral organs and fruits, is found in other species of *Corydalis* such as *C. aurea* and *C. Caseana*.

Plants of ssp. *australis* from coastal North Carolina, South Carolina, and Georgia are appreciably smaller and more strict in habit than those from other parts of the range of the subspecies. The flowers also are noticeably smaller, the hood is not crested, and the fruits are very slender and often moniliform.

The center of diversity of this subspecies is eastern Oklahoma and southeastern Missouri, and plants intermediate between this subspecies and ssp. *micrantha* and

C. curvisiliqua are not uncommonly collected in this area. The disposition of a given specimen, however, ordinarily is not difficult.

In disturbed, often sandy soil, abandoned fields and waste areas, along roadsides, and in open woods; from southern Missouri and eastern Kansas to Texas, Florida, and North Carolina. Flowers in early spring, about February 15 to April 30; fruits from about March 1 to May 15.



Map 8. Distribution of *Corydalis micrantha* (Engelm.) Gray ssp. *australis* (Chapm.) Ownbey.

NORTH CAROLINA: Bladen, Brunswick, Craven, Jones, Lenoir, and New Hanover counties.

SOUTH CAROLINA: Beaufort, Charleston, Georgetown, and Horry counties.

GEORGIA: Camden, Glynn, and Pulaski counties.

FLORIDA: Alachua, Duval, Franklin, Hernando, Leon, Marion, Nassau, Putnam, and St. John counties.

ALABAMA: Mobile County.

MISSISSIPPI: Harrison County.

LOUISIANA: Jefferson, Natchitoches, Orleans, and Rapides parishes.

TEXAS: Anderson, Austin, Bastrop, Bell, Brazos, Burleson, Caldwell, Clennan, Dallas, DeWitt, Frio, Galveston, Gonzales, Grayson, Gregg, Harris, Henderson, Jackson, Kaufman, McLennan, Nueces, Rusk, San Augustine, Smith, Tarrant, Travis, Upshur, Victoria, Waller, Washington, and Wharton counties.

OKLAHOMA: Carter, Cleveland, Creek, Logan, Murray, Muskogee, Oklahoma, Payne, and Pottawatomie counties.

ARKANSAS: Benton, Crawford, Hempstead, Hot Spring, Jackson, and Pulaski counties.

MISSOURI: Barry, Carter, Cedar, Dunklin, Jackson, Jefferson, Madison, Mississippi, St. Clair, Scott, and Vernon counties.

KANSAS: Miami County.

7b. CORYDALIS MICRANTHA (Engelm.) Gray ssp. **texensis** G. B. Ownbey, ssp. nov.

Herbae annuae glaucae; caulibus 20–45 cm. longis saepe crassis post exsiccationem valde striatis; foliorum laminis pinnatis, segmentis primariis pinnatifidis incisis ultimis oblongo-acutis subapiculatis; racemis saepe crassis folia superantibus, bracteis ovato-attenuatis margine denticulatis infimis ca. 5 mm. longis 2 mm. latis superioribus aliquid minoribus; floribus flavis primo congestis in anthesim remotioribus, pedicellis erectis patulisve 2–4 mm. longis, sepalis fugaceis ca. 1.5 mm. longis ovato-attenuatis, petalo calcarato valde arcuato 12–15 mm. longo carinae cristo satis humili undulato margine bene manifesto supra cristum inflexo calcare obtuso haud globoso, petalo ecalcarato exteriori ca. 10 mm. longo margine haud reflexo duobus interioribus 8–10 mm. longis oblanceolatis ungui 3–4 mm. longo, lamina apice quam basi multo latiori, calcare staminali ca. 2 mm. longo clavato, stigmate 2-lobato ca. bis longiori latiori; fructibus erectis vel incurvatis gracilibus 25–30 mm. longis; seminibus ca. 1.5 mm. diam. sub lente aliquid ornatis margine obtuso.

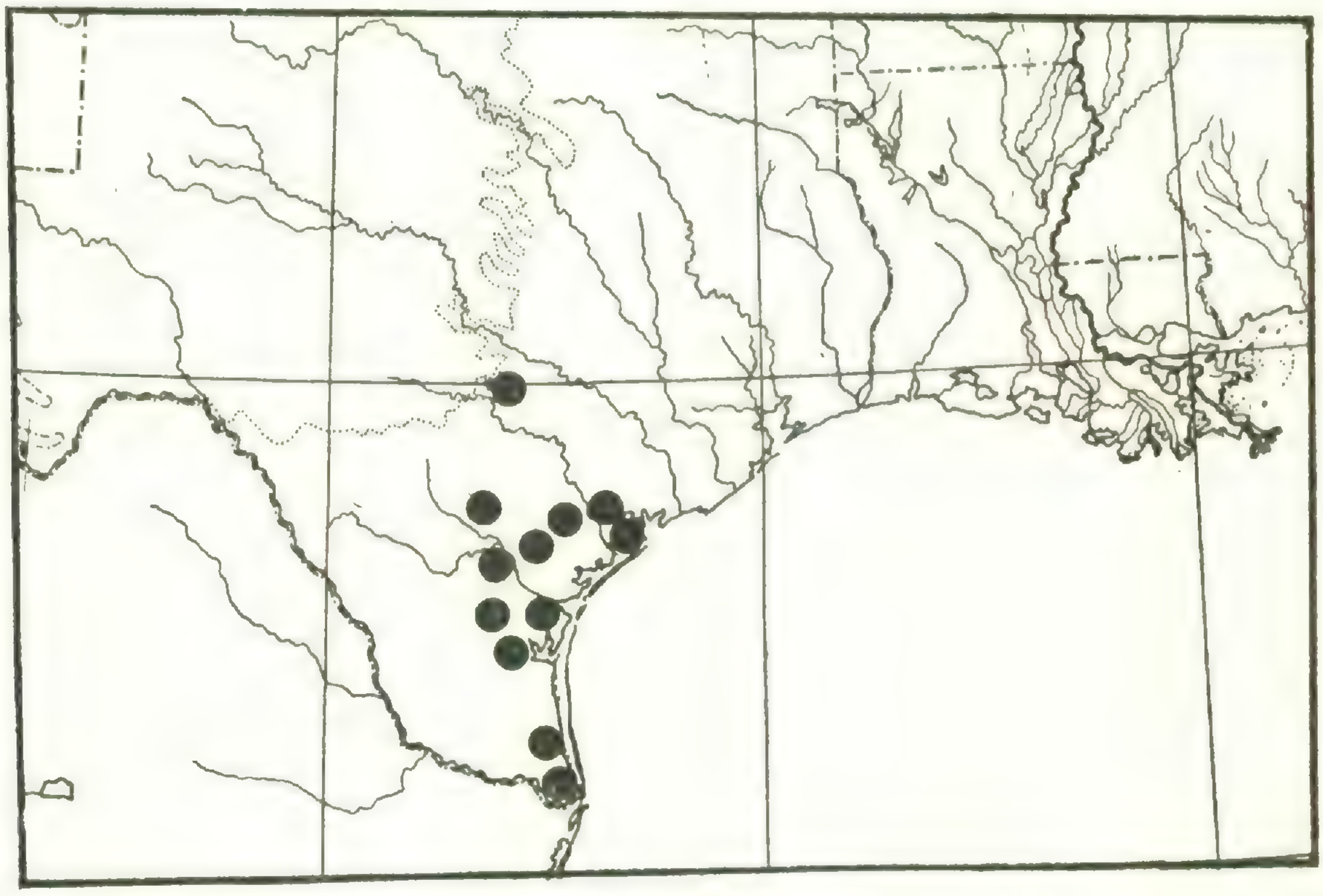
Glaucous annual; stems 20–45 cm. long, often stout and strongly striate when dry, prostrate-ascending; leaf blades pinnate, the primary segments pinnatifid and again incised, the ultimate lobes oblong-acute, subapiculate; racemes often stout, surpassing the leaves; bracts ovate-attenuate, denticulate at the margin, the lowermost about 5 mm. long and 2 mm. broad, the upper somewhat reduced; pedicels erect or spreading, 2–4 mm. long; sepals fugacious, about 1.5 mm. long, ovate-attenuate; flowers yellow, crowded at first, becoming more distant during anthesis; spurred petal strongly arcuate, 12–15 mm. long, the hood with a low undulate crest, the wing margin well developed, reflexed upon the hood, the blunt spur 5–7 mm. long, not globose; spurless outer petal about 10 mm. long, the margin not reflexed; inner petals 8–10 mm. long, oblanceolate, the claw 3–4 mm. long, the blade much broader at the apex than at the base; stamen spur about 2 mm. long, clavate; stigma 2-lobed, twice as broad as high; fruits erect or incurved, slender, 25–30 mm. long; seeds about 1.5 mm. in diameter, moderately decorated under magnification, obtuse at the border, with no ring margin.

This well-defined subspecies is endemic to the coastal plain of southern Texas. It is most closely comparable to ssp. *australis*, but is easily distinguished by its longer fruits and more strongly arcuate spurred petal. In habit and foliage it is very similar to *C. curvisiliqua* ssp. *curvisiliqua* with which it is often confused. It can be distinguished from the latter by its non-muricate seeds and shorter spur which is not globose at the tip.

Moist, often sandy soil, open ground of alluvial plains and uplands; south coastal Texas. Flowers in early spring from about February 20 to March 20; fruits from about March 1 to April 10.

TEXAS: ATASCOSA CO.—moist, alluvial ground, Campbelton, March 10, 1917, *Palmer 11239* (M, G, US). BEE CO.—Beeville, March 30, 1932, *Jones 29365* (M, TYPE). CALHOUN CO.—Bahia del Espiritu-Santo, ex herb. *Berlandier 548, 1799, 1933* (G). CAMERON

co.—Palm Grove, March 3, 1940, *Parks 1429* (M). GOLIAD CO.—Goliad, Feb., 1927, *Williams 11* (UT). JIM WELLS CO.—sandy loam, about 600 ft. alt., Romarsid Ranch, March 18, 1943, *Freeborn 338* (UT). KENDALL CO.—Edge Falls, March 26, 1938, *Parks 29500* (G). KLEBERG CO.—Riviera, Feb. 22, 1930, *Harrison* (US). LIVE OAK CO.—sandy upland, 41 mi. n. of Alice, March 1, 1944, *Painter & Barkley 14461* (UT). NUECES CO.—Corpus Christi, May, 1913, *Orcutt 5829* (M); Robstown, March 26, 1920, *High 91* (M). VICTORIA CO.—Victoria, April 6, 1900, *Eggert* (M); sandy, open ground, Victoria, March 4, 1916, *Palmer 9064* (M, D, US); Victoria-Goliad, March 29, 1930, *Tharp* (UT). WILLACY CO.—in open ground, sandy situations, March 21, 1937, *Runyon 1618*.



Map 9. Distribution of *Corydalis micrantha* (Engelm.) Gray ssp. *texensis* Ownbey.

8. C. CURVISILIQUA Engelm. ssp. **curvisiliqua** G. B. Ownbey, stat. nov.

Corydalis aurea var. *curvisiliqua* Gray, in Proc. Acad. Phila. **1863**:57. 1864, nom. nud.
Corydalis curvisiliqua Engelm. ex Gray, l. c. 1864, nom. nud. in synon.; apud Gray, Man. Bot. ed. 5: 62. 1867; Bot. Gaz. **11**:188. 1886.
Capnoides curvisiliqua Ktze. Rev. Gen. **1**:14. 1891.
Neckeria curvisiliqua Rydb. in Univ. Nebr. Bot. Surv. Nebr. **3**:24. 1894.

Glaucous winter annual or perhaps biennial; stems 1–several, the primary often erect, the 1–several secondary ascending, 10–40 cm. long, often somewhat branched; basal leaves long-petioled; cauline leaves short-petioled, reduced in size; leaf blades pinnate, the pinnae twice pinnatifid, rarely again incised, the ultimate segments oblong, obtuse or rounded; peduncles usually surpassing the leaves, the primary 6- to 18-, usually about 12-flowered; the secondary fewer-flowered; bracts ovate, 10 mm. or less long, 6 mm. or less wide, the lowest sometimes foliose, much reduced upward; pedicels stout, spreading, 2–3 mm. long; sepals scarious,

broadly ovate to ovate-attenuate, often more or less toothed or undulate at the margin, about 1 mm. long; flowers bright yellow, often strongly arcuate, crowded on the raceme at first, becoming more distant during anthesis; spurred petal 16–18 mm. long, with a very broad wing margin, the crest absent to well developed and undulate or toothed, the spur 7–9 mm. long, often somewhat globose at the blunt tip; spurless outer petal 12–15 mm. long, geniculate, about 3 mm. longer than the inner petals, the crest similar to that of the spurred petal; inner petals oblanceolate, 9–11 mm. long, the slender claws nearly half the total length; stamen spur clavate, bent near the apex, 4–6 mm. long; stigma 2-lobed, twice as broad as high; style slender; fruits slender, erect, moderately to strongly arcuate or incurved toward the floral axis, usually 26–34 mm. long; seeds about 2 mm. in diameter, black, muricate, with essentially no ring margin at maturity.

Subspecies *curvisiliqua* is most easily recognized by its extremely long, erect, incurved fruits, and its seeds which are distinctly muricate under magnification. The latter character is approached nowhere else in the genus, and, indeed, is the strongest character upon which the species is based. The tetragonal character of the fruits mentioned by Gray (Bot. Gaz. **11**:189. 1886), although perhaps more pronounced here, especially in fresh material, is by no means unique.

Floral characters which are of value in recognizing this subspecies are the well-developed wing margins of the outer petals, the much-reduced, claw-like basal portion of the unspurred outer petal, and the well-developed spur which is about one-half the total length of the spurred petal. The degree to which the crest is developed is extremely variable; material from the type locality usually has no apparent crest. Some plants, however, have a moderately well developed crest. This diversity is general throughout the range of the subspecies.

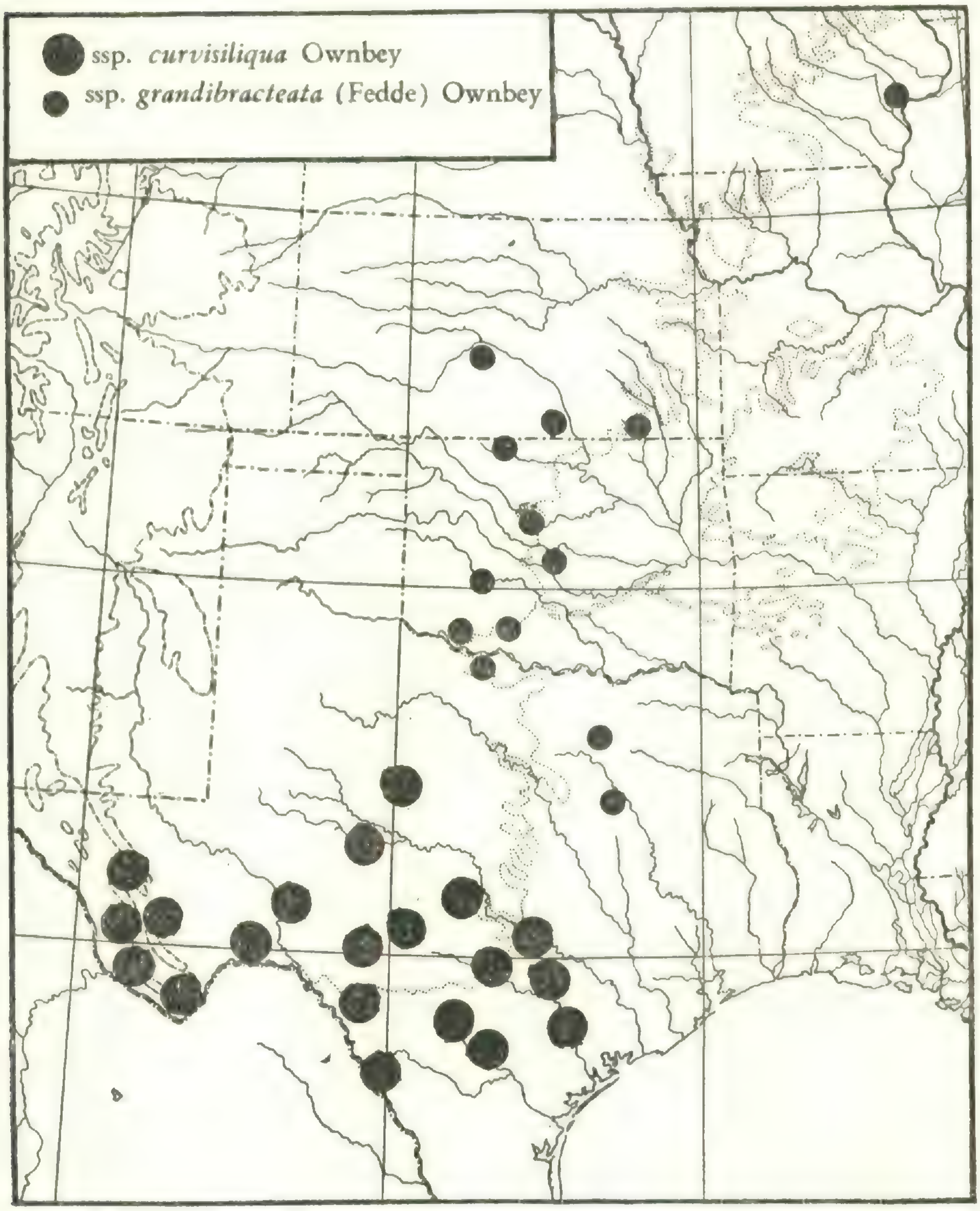
Disturbed soil, sandy bottoms, abandoned fields, open woods, hillsides, and valleys; central to western Texas. Flowers in early spring from about March 1 to May 1; fruits from about March 15 to May 15.

TEXAS: Bexar, Brewster, Caldwell, Comal, Crockett, Culberson, Edwards, Frio, Gillespie, Hays, Irion, Jeff Davis, Karnes, Kerr, Kinney, Llano, Maverick, Medina, Presidio, Taylor, Terrell, Tom Green, Travis, and Uvalde counties.

8a. C. CURVISILIQUA Engelm. ssp. **grandibracteata** (Fedde) G. B. Ownbey, stat. nov.

Corydalis curvisiliqua var. *grandibracteata* Fedde, Rep. Spec. Nov. **11**:291. 1912.

Glaucous winter annual; stems 1–several, stout, ascending, commonly 20–30 cm. long; basal leaves numerous, moderately long-petioled; cauline leaves somewhat reduced, shorter-petioled; leaf blades pinnate, the primary segments pinnatifid and usually again incised, the ultimate segments elliptical to obovate; peduncles stout, surpassing the leaves; bracts conspicuous, usually ovate-acuminate, the lowermost usually 10–15 mm. long and 4–6 mm. wide, somewhat reduced upward; pedicels spreading, usually 2–3 mm. long; sepals ovate, variously toothed; flowers bright yellow; spurred petal 15–18 mm. long, having a well-developed wing margin, the hood crested, the crest conspicuous, regular or undulate, the stout spur 7–9 mm.



Map 10. Distribution of *Corydalis curvisiliqua* Engelm.

long, somewhat globose at the tip; spurless outer petal 12–15 mm. long, geniculate, the basal portion slender, claw-like, the crest similar to that of the spurred petal; inner petals oblanceolate, 9–11 mm. long, the claw slender, 4–5 mm. long; stamen spur about two-thirds the length of the petal spur; stigma twice as broad as high; style slender; fruits slender, erect, incurved toward the floral axis, 20–25 mm. long, gradually tapered apically; seeds about 2 mm. in diameter, black, having a narrow ring margin, distinctly muriculate under magnification.

This subspecies is best distinguished by its slender, lanceolate, erect, incurved fruits, its relatively large flowers, the usually highly developed crest and wing margin, and the large ovate floral bracts. The muriculate character of the seeds, so striking in ssp. *curvisiliqua,* is here reduced nearly to the condition found in *C. aurea* ssp. *occidentalis*. Hybridization between the two and with *C. micrantha* ssp. *australis* may account for the anomalous nature of many specimens. However, because of the greatest agreement in floral morphology with *C. curvisiliqua* and because its range is a northward extension of that species I believe that it is properly placed here.

The isolated occurrence of ssp. *grandibracteata* in Muscatine Co., Iowa, perhaps is best explained by a chance introduction of seeds.

Usually in sandy soil, open ground, alluvial plains, roadsides, prairies, and slopes; southern Kansas to northern Texas; eastern Iowa. Flowers from about April 15 to May 15; fruits from about May 1 to May 30.

IOWA: Muscatine County.

KANSAS: Chautauqua, Stafford, and Sumner counties.

OKLAHOMA: Alfalfa, Caddo, Canadian, Cleveland, Comanche, Grady, Kingfisher, Kiowa, Logan, McClain, Oklahoma, and Stephens counties.

TEXAS: Archer, Clay, Collin, Dallas, and Navarro counties.

9. C. AUREA Willd. ssp. **aurea** G. B. Ownbey, stat. nov.

Corydalis aurea Willd. Enum. Hort. Berol. **2**:740. 1809.
Fumaria aurea Muhl. ex Willd. l. c. 1809, as syn.
Fumaria aurea Ker, Bot. Reg. **1**:*t. 66*. 1815.
Odoptera aurea Raf. Cat. 15. 1824.
Corydalis montana Engelm. ex Gray, in Mem. Am. Acad. **4**:6. 1849, nom. nud. in synon.
Corydalis aurea var. *typica* Regel, in Mem. Acad. St. Petersb. 4^4:19. 1861 (Tent. Fl. Ussuri. 19. 1861); Bull. Soc. Mosc. 34^3:145. 1861.
Corydalis aurea var. *parviflora* Regel, in Bull. Soc. Mosc. 34^3:146. 1861.
Corydalis aurea β. *macrantha* Wood, Am. Bot. & Fl. 34. 1870.
Capnodes aureum Ktze. Rev. Gen. **1**:14. 1891.
Neckeria aurea Millsp. Fl. W. Va. 327. 1892 (W. Va. Agr. Exp. Sta. Bull. 2).
Corydalis Wetherillii Eastw. in Bull. Torr. Bot. Club **29**:524. 1902.
Corydalis wyomingensis Fedde, Rep. Spec. Nov. **10**:312. 1912.
Corydalis tortisiliqua Fedde, l. c. 313. 1912.
Corydalis Gooddingii Fedde, l. c. 1912.
Corydalis hypecoiformis Fedde, l. c. 314. 1912.
Corydalis Engelmannii Fedde, l. c. 365. 1912.
Corydalis aurea var. *robusta* Fedde, l. c. 379. 1912.
Corydalis monilifera Fedde, l. c. 417. 1912.
Corydalis washingtoniana Fedde, l. c. 419. 1912.
Corydalis macrorrhiza Fedde, l. c. 479. 1912.
Corydalis Albertae Fedde, l. c. **11**:196. 1912.
Corydalis Jonesii Fedde, l. c. 1912.

Corydalis oregana Fedde, l. c. 290. 1912.
Corydalis densicoma Fedde, l. c. 291. 1912.
Capnoides Wetherillii Heller, in Muhlenbergia 7:123. 1912.
Capnoides euchlamydeum Woot. & Standl. in Contr. U. S. Nat. Herb. 16:122. 1913.
Corydalis tortisiliqua var. *longibracteata* Fedde, l. c. 11:497. 1913.
Corydalis Engelmannii var. *exaltata* Fedde, l. c. 1913.
Corydalis isopyroides Fedde, l. c. 498. 1913.
Corydalis isopyroides var. *Mearnsii* Fedde, l. c. 12:37. 1913.
Corydalis wyomingensis var. *lativaginata* Fedde, l. c. 38. 1913.
Capnoides Engelmannii Cockerell, in Univ. Colo. Stud. 11:216. 1915.
Capnoides macrorrhiza Cockerell, l. c. 1915.
Corydalis euchlamydea Fedde, l. c. 18:32. 1922.

Glaucous winter annual or biennial from a more or less branched caudex; stems sympodial, prostrate-ascending, 10–50, usually 20–35 cm. long; basal leaves long-petioled; cauline leaves barely reduced in size upward, also usually long-petioled; leaf blades pinnate, with 5–7 pinnae, these pinnatifid into about 5 segments which are again incised; ultimate leaf segments broadly to narrowly elliptical, 1.5–several times as long as broad, greatly variable in gross size, subapiculate; peduncles short, terminal; racemes shorter than to barely exceeding the leaves, the primary 10- to 30-, usually 10- to 20-flowered, the secondary 4- to 12-flowered; bracts elliptical to linear, the lowest 4–10 mm. long and 1–2 mm. broad, rarely larger, often denticulate at the apex, much reduced upward; pedicels erect when young, generally reflexed or recurved in fruit, the lowermost 5–10 mm. long; sepals scarious, fugacious, broadly ovate or ovate-attenuate, irregularly toothed, 1–3 mm. long; flowers pale to bright yellow; spurred petal 13–16 mm. long, the hood usually not crested, the crest when present low and incised, the wing margin moderately to well developed, the spur straight or slightly incurved, 4–5 mm. long, the tip somewhat globose; spurless outer petal 9–11 mm. long, the hood and crest as in the spurred petal; inner petals 8–10 mm. long, the claw 3.5–4.5 mm. long, the blade somewhat broader and more distinctly winged distally; stamen spur 2–3 mm. long; stigma about twice as broad as high; fruits commonly 18–24, rarely up to 30 mm. long, usually slender, often erect when young, generally pendent at maturity, straight to moderately arcuate, often moniliform, the valves often torulose when dry; seeds nearly 2 mm. in diameter, black, shiny, turgid, obscurely decorated to nearly smooth under magnification, broadly acute at the edge, with no ring margin.

This subspecies is best distinguished on the basis of the generally weak racemes and slender, pendent or spreading fruits. The racemes ordinarily do not exceed the leaves except in early stages of growth. It intergrades at times with ssp. *occidentalis*, but in general can be distinguished without difficulty when the plant is in fruiting condition.

Contingent upon the broad view of the subspecies adopted here it has been necessary to reduce to synonymy a large number of specific and varietal epithets proposed by Fedde. For the most part, they are founded upon minor variant forms which are by no means mutually exclusive. A brief discussion of the proposed

biological basis for the type of variability found in *C. aurea* is given in the introductory material to this paper.

Corydalis aurea ssp. *aurea* is of north temperate and subarctic distribution. In the northern part of its range it is found at low elevations, but in the southern part it is confined largely to mountainous districts, and may grow at elevations of 11,000 feet or more. Consequent to its wide range and adaptation to a diversity of habitats, this subspecies has become quite polymorphic. It seems probable that a good deal of minor genetic differentiation has taken place in each of the isolated mountain ranges of the Southwest. Ultimately the many forms thus produced may be of nomenclatorial rank. At present their nomenclatorial recognition can add nothing to an understanding of the group.

Among the many recognizable variants which in my opinion are not nomenclatorially important the following are mentioned briefly:

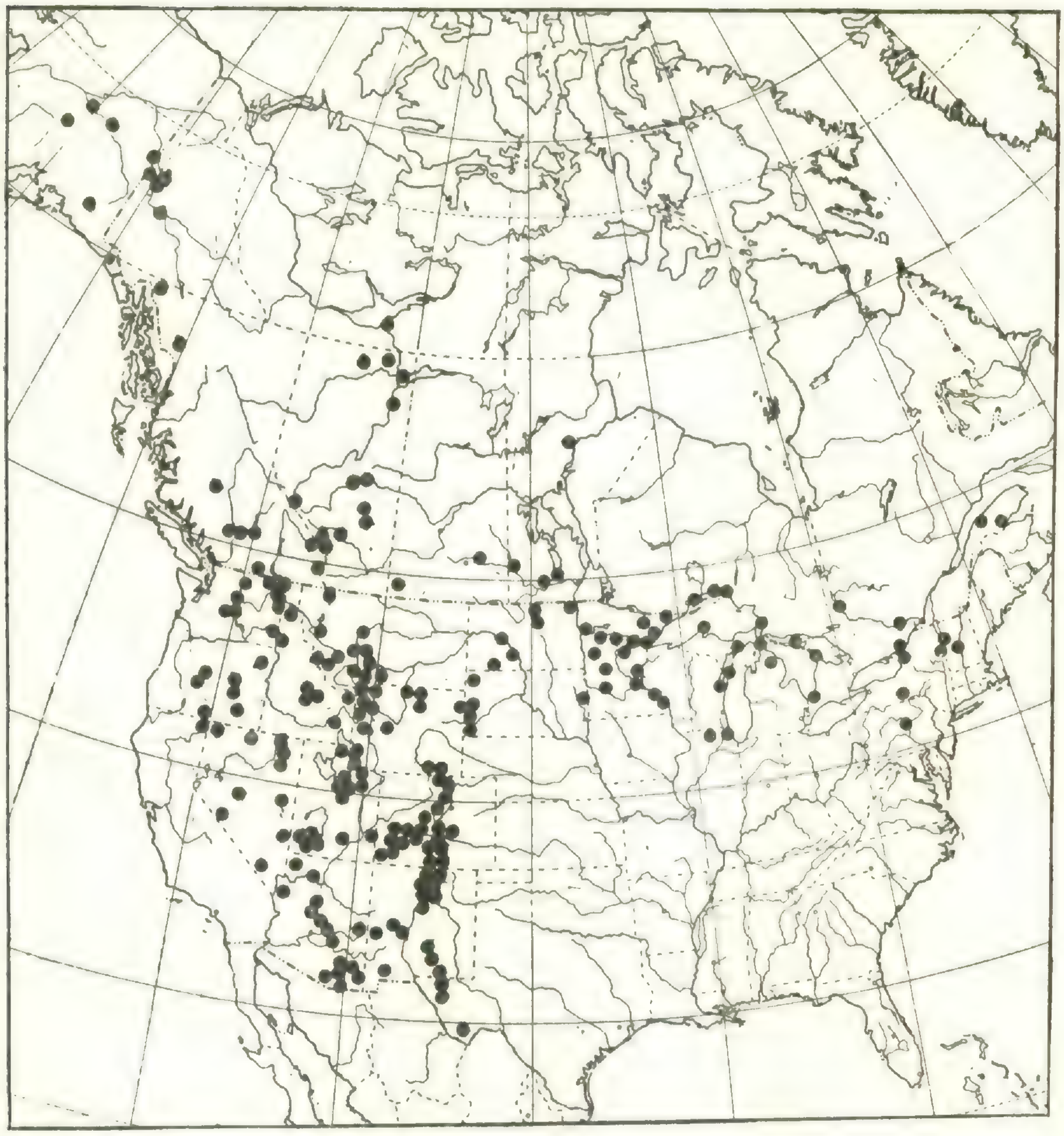
Plants from Rimouski County, Quebec, described as *C. aurea* var. *robusta* by Fedde, are of interest primarily because of their very foliose stems. Plants with similar foliage are found in southeastern Canada and northern United States as far west as the shores of Lake Superior and Lake Michigan. Fruit characters emphasized by Fedde do not set these plants apart from the subspecies proper.

At low elevations in Washington, Oregon, Idaho, Nevada, and Wyoming plants sometimes are found with stout stems, semi-erect fruits, and short, obtuse ultimate segments of the basal leaves. These are all better placed with ssp. *aurea* because of the unreliability and probable superficiality of the distinguishing characters.

In the mountains of Otero and Lincoln counties, New Mexico, is a variant having very large, foliose bracts. In fruit characters it is intermediate between ssp. *aurea* and ssp. *occidentalis*. This variant was described as *Capnoides euchlamydeum* by Wooton and Standley, but I cannot see that the differences are in any way essential, and am therefore reducing the name to synonymy.

Particularly striking variant forms having weak, diffusely branched, leafy stems, weak, 1- to 4-flowered racemes, and very broad, incompletely divided ultimate leaf segments occur sporadically throughout the Southwest. Among many localities where plants of this description are found may be mentioned especially Crandall Canyon, Carbon County, Utah, the Charleston Mts., Clark County, Nevada, the Grand Canyon National Park, Arizona, the Santa Catalina and Chiricahua Mts., Arizona, the Black Range, Grant and Sierra counties, New Mexico, the Guadalupe Mts., Culberson County, Texas, and the Davis Mts., Jeff Davis County, Texas. The tendency for plants of this sort to be produced, therefore, is widespread. Viewed separately they often appear significantly different, but against the background of the subspecies proper their significance fades.

Although the outer petals of ssp. *aurea* ordinarily are not crested, an occasional exception to this generalization is met with in northern and western United States. The fact that the presence of a crest apparently is not tied up with any constant morphological difference, together with its erratic occurrence, leads me to believe that it does not warrant serious consideration.



Map 11. Distribution of *Corydalis aurea* Willd. ssp. *aurea* Ownbey.

Loose, open, often gravelly soil, lake shores, talus slopes, ledges, rocky hillsides and creek bottoms, gravel pits, road cuts, and burned-over areas; northeastern United States, northward and westward to Quebec, the Dakotas, Mackenzie, and Alaska, southward in the Rocky Mountains to Arizona, New Mexico and western Texas, at elevations of a few hundred feet in northern United States and Canada to over 11,000 feet in the Colorado Rockies. Flowers throughout the summer months, from about May 1 to August 30; fruits from about May 15 to September 15.

PENNSYLVANIA: Snyder County.

NEW YORK: Essex, Jefferson, and Tompkins counties.

VERMONT: Addinson, Chittenden, Rutland, and Windsor counties.

NEW HAMPSHIRE: Grafton County.

ILLINOIS: Cook and Winnebago counties.

MICHIGAN: Alpena, Keewenaw, Mackinac, Montmorency, Oscoda, and Schoolcraft counties.

WISCONSIN: Brown and Door counties.

MINNESOTA: Aitkin, Becker, Beltrami, Carlton, Cass, Chisago, Clearwater, Cook,

Crow Wing, Dakota, Goodhue, Hennepin, Hubbard, Lake, Meeker, Ottertail, Polk, Pope, Ramsey, Renville, St. Louis, Todd, Wabasha, and Winona counties.

SOUTH DAKOTA: Brookings, Custer, Fall River, Harding, Lawrence,. Meade, and Pennington counties.

NORTH DAKOTA: Benson, McLean, Morton, Pembina, and Rolette counties.

MONTANA: Carbon, Cascade, Chouteau, Deerlodge, Flathead, Gallatin, Jefferson, Lewis & Clark, Meagher, Missoula, Park, Powell, and Ravalli counties; Glacier National Park.

WYOMING: Albany, Big Horn, Crook, Fremont, Johnson, Lincoln, Park, Sheridan, Sublette, Teton, and Uinta counties; Yellowstone National Park.

COLORADO: Boulder, Chaffee, Clear Creek, Conejos, Custer, El Paso, Fremont, Gilpin, Grand, Gunnison, Hinsdale, Jefferson, Lake, La Plata, Larimer, Mineral, Montezuma, Montrose, Ouray, Park, Pueblo, Rio Grande, Saguache, San Juan, Summit, Teller, and Weld counties; Rocky Mountain National Park.

NEW MEXICO: Bernalillo, Catron, Colfax, Dona Ana, Eddy, Grant, Lincoln, Luna, Mora, Otero, Rio Arriba, Sandoval, San Miguel, Santa Fe, Sierra, Socorro, and Taos counties.

TEXAS: Brewster, Culberson, and Jeff Davis counties.

ARIZONA: Apache, Cochise, Coconino, Gila, Graham, Mohave, Pima, and Yavapai counties; Grand Canyon National Park.

UTAH: Beaver, Cache, Carbon, Daggett, Duchesne, Garfield, Iron, Salt Lake, San Juan, San Pete, Summit, Uintah, Utah, and Wasatch counties.

NEVADA: Clark, Elko, Esmeralda, Humboldt, Lincoln, Nye, and White Pine counties.

CALIFORNIA: Modoc County.

IDAHO: Bannock, Blaine, Bonner, Clark, Custer, Fremont, Kootenai, and Owyhee counties.

OREGON: Crook, Grant, Harney, Lake, and Wallowa counties.

WASHINGTON: Chelan, Douglas, Ferry, Kittitas, Okanogan, Pend Oreille, Spokane, Stevens, and Whitman counties.

QUEBEC: BONAVENTURE CO.—Restigouche River, Matapedia, Aug. 1, 1936, *Victorin, Germain & Dominique 48996* (UO, UC, CIUC, G). RIMOUSKI CO.—Massacre Island, on conglomerate covered with moss, coniferous woods, Bic, Aug. 12, 1927, *Rousseau 26871* (US); same locality, June 30, 1927, *Rousseau 26401* (M, WS, G); humus in crevices of calcareous rock, July 8, 1905, *Collins & Fernald 85* (G, UC, NY, US). TEMISCAMING DIST.—Point-au-vent (Lake Temiscaming), June 25, 1918, *Victorin 8358* (M, G, US). WRIGHT CO.—Aylmer, May 26, 1901, *Fowler* (US).

ONTARIO: ALGOMA DIST.—waste ground by Algoma Central Railway, Gray (Mile 229), June 23, 1921, *Pease 18029* (G); ballast near Coppermine Point, Lake Superior, July 7, 1935, *Pease & Ogden 25161* (G). BRUCE CO.—Lion's Head, on damp calcareous rocks, June 11, 1932, *Victorin & Prat 45945* (RM, G). CARLETON CO.—vicinity of Ottawa, May 28, 1921, *Rolland 15761* (WS, NY, US). FRONTENAC CO.—Gardiner's Farm, near Kingston, June 10, 1897, *Langford* (M). LAMBTON CO.—on sides of sand hills, near Port Franks, May 24, 1906, *Dodge 1* (US). MANITOULIN CO.—dry cliffs, Gore Bay, Manitoulin Island, July 5, 1935, *Pease & Ogden 25190* (G, US). THUNDER BAY DIST.—rich shore of Lake Superior, about Lat. 48° 45′ N., Long. 87° 15′ W., 1 mi. n.e. of Schreiber, Aug. 16, 1937, *Hosie, Losee & Bannan 1413* (G); damp diabase ledge, Norma Creek, Thunder Cape, June 26, 1936, *Taylor, Losee & Bannan 504* (CIUC).

MANITOBA: MARQUETTE DIST.—Fort Ellice, along the line of the Grand Trunk Pacific Railway, June 27, 1906, *Macoun & Herriot* (G). PORTAGE LA PRAIRIE DIST.—Portage la Prairie, along the line of the Grand Trunk Pacific Railway, May 28, 1906, *Herriot* (G); Carberry, 1898, *Thompson* (M). DIST. UNCERTAIN—Piguitonay, Mile 214, route of Hudson Bay Railway, July 8, 1917, *Emerton* (G); Charleswood, June 5, 1915, *Thompson 97* (M).

SASKATCHEWAN: MOOSE JAW DIST.—newly burnt woods, Cypress Hills, June 15, 1884, *Macoun* (G). QU'APPELLE DIST.—moist woods, Qu'Appelle Valley, June 26, 1938, *Shevkenek 115* (G). DIST. UNCERTAIN—in rich, moist ground, usually in burnt-over ground, McKague, June 21, 1940, *Breitung 577* (M, IH, UT, NY).

ALBERTA: CALGARY DIST.—gravel banks and rocky hills, Shaganappi, vicinity of Calgary, 3400–3600 ft. alt., May 30, 1913, *Moodie 137* (NY, US). EDMONTON DIST.—burned area in woods, Edmonton, May 21, 1931, *Moss 2140* (WS). JASPER NAT. PARK—Jasper, 3472 ft. alt., Aug. 31–Sept. 2, 1943, *Scamman 3369* (G, US). MEDICINE HAT DIST.—moist, rocky woods, vicinity of Rosedale, 2200–2500 ft. alt., May 27, 1915, *Moodie 911* (M, CIUC, D, UT, NY, G, US). RED DEER DIST.—n. e. of Buffalo Lake, May 23, 1926, *Brinkman 2015* (US); Sarcee Reserve, June 15 to Aug. 15, 1905, *Goddard 489* (UC). ROCKY MTS. NAT. PARK—Bow River Valley, 4500 ft. alt., Banff, June 9–18, 1906, *Brown 62* (M, NY, G, US); roadside near the village, vicinity of Banff, 4500 ft. alt., June 19, 1899, *McCalla 2124* (NY, US). VICTORIA DIST.—grain field, Fort Saskatchewan, June 10, 1930, *Turner* (G). DIST. UNCERTAIN (probably ATHABASKA)—Athabaska Landing, July 28, 1914, *Hitchcock 12064* (US); Fort Chipewyan, Athabaska, June 5, 1903, *Preble & Cary 5* (US); muddy river bank along lower Firebag River near its mouth, June 3, 1935, *Raup 6033* (G); base of eastern slope of Caribou Mts., about 58° 57′ N., 113° 55′ W., and 58° 51′ N., 113° 57′ W., Wood Buffalo Park, Mackenzie Basin, July 17, 1930, *Raup 2439-a* (NY, US).

BRITISH COLUMBIA: CARIBOO DIST.—Alexis Creek, June, 1914, *Newcombe 19* (G). CASSIAR DIST.—above Discovery on road to Surprise Lake, July 10, 1930, *Setchell & Parks* (UC); near head of Ingenika River, Sept. 8, 1910, *Preble & Mixter 689b* (US); near head Iskut River, July 29, 1910, *Preble & Mixter 601* (US). KOOTENAY DIST.—near Goat Creek, 27 mi. n. of Natal, July 4, 1941, *Weber 2296* (M, RM, WS, NY, G); Kicking Horse Valley, vicinity of Field, 4000 ft. alt., June 20, 1906, *Brown 214* (M, NY, G, US). YALE DIST.—near Guichon Creek, 13 mi. s. of Savona, 50° 32′ N., 120° 52′ W., about 3500 ft. alt., June 23, 1941, *Hitchcock & Martin 7412* (M, RM, WS, UC, IH, NY, G); along Bolean Creek, about 1 mi. n.w. of Falkland, 2400 ft. alt., June 30, 1941, *Hitchcock & Martin 7485* (M, RM, WS, UC, IH, NY, G).

MACKENZIE: Fort Resolution, no date, *Onion, Kennicott & Hardisty* (NY).

YUKON: Fifty-Mile River, Aug. 4, 1899, *Bolton* (US); Dawson, June 3, 1914, *Eastwood 133* (WS, CIUC, G, US); recent burns, Fort Selkirk, June 13, 1899, *Gorman 1023* (NY, US); Klondyke, 1900, *MacLean* (US); Bonanza Creek, Aug. 11, 1899, *Tarleton 40b* (NY, US); Walker Gulch, July 16, 1899, *Williams* (NY); Lake Lebarge, June 23, 1899, *Tarleton 49a* (NY, US).

ALASKA: Eagle to Valdes trail, June 30, 1902, *Collier 73* (US); vicinity of Copper Center, 1908, *Heideman 66* (US); Hot Springs on the Tanana River, July 28, 29, 1909, *Hitchcock* (US); Yukon River country, no date, *Ketchum* (G); banks of railroad cut, Mt. McKinley Nat. Park, Aug. 2, 1939, *Nelson & Nelson 4010* (M, RM, NY, G); Fairbanks, June, 1927, *Palmer 1750* (US); Gopher Center, Copper River region, June 1, 1902, *Poto 14* (US).

9a. C. AUREA Willd. ssp. **occidentalis** (Engelm.) G. B. Ownbey, stat. nov.

Corydalis aurea var., Gray in Smiths. Contr. Knowl. **5**:10. 1853 (Pl. Wright. **2**:10).
Corydalis montana Engelm. apud Gray, Man. Bot. ed. 5. 62. 1867.
Corydalis aurea var. *occidentalis* Engelm. apud Gray, l. c. 1867; Bot. Gaz. **11**:188. 1886.
Capnoides montanum Britton, in Mem. Torr. Bot. Club **5**:166. 1894.
Neckeria aurea occidentalis Rydb. in Univ. Nebr. Bot. Surv. Nebr. **3**:24. 1894.
Corydalis crassipedicellata Fedde, Rep. Spec. Nov. **10**:364. 1912.
Corydalis bilimbata Fedde, l. c. 379. 1912.
Corydalis chihuahuana Fedde, l. c. 418. 1912.
Corydalis curvisiliquaeformis Fedde, l. c. **11**:289. 1912.
Corydalis Jonesii var. *stenophylla* Fedde, l. c. 497. 1913.
Corydalis pseudomicrantha var. *Griffithsii* Fedde, l. c. **12**:37. 1913.
Corydalis pachyloba Fedde, l. c. 38. 1913.
Capnoides pachylobum Greene ex Fedde, l. c. 1913, nom. nud. in synon.

Glaucous winter annual or biennial; stems often erect while young, usually 10–25 cm. or more long; basal leaves long-petioled; cauline leaves few, often some-

what reduced in size; leaf blades pinnate, having 5–7 pinnae, these pinnatifid and again incised; ultimate leaf segments usually oblong, 2–5 times longer than broad, subapiculate; peduncles usually stout; racemes surpassing the leaves at least in the early stages of growth, 5- to 20-, usually 8- to 12-flowered; bracts elliptical to linear, 10 mm. or less long, much reduced upward; pedicels erect, 1–5 mm. long; sepals scarious, fugacious, ovate, often toothed at the margin, 2 mm. or less long; flowers mostly bright yellow; spurred petal 14–18 mm. long, the hood usually not crested, the wing margin well developed, the blunt spur 5–9 mm. long, often somewhat globose at the tip; spurless outer petal 8–13 mm. long, geniculate, the hood and margin as in the spurred petal; inner petals 8–11 mm. long, the claw about one-half of the total length; stamen spur 3–6 mm. long; stigma about twice as broad as high; fruits 12–30, commonly 16–18 mm. long, erect, stout, curved upward and inward or obliquely along the floral axis, not moniliform; seeds about 2 mm. in diameter, black, acute at the edge, usually having a narrow marginal ring which is distinctly reticulate under magnification.

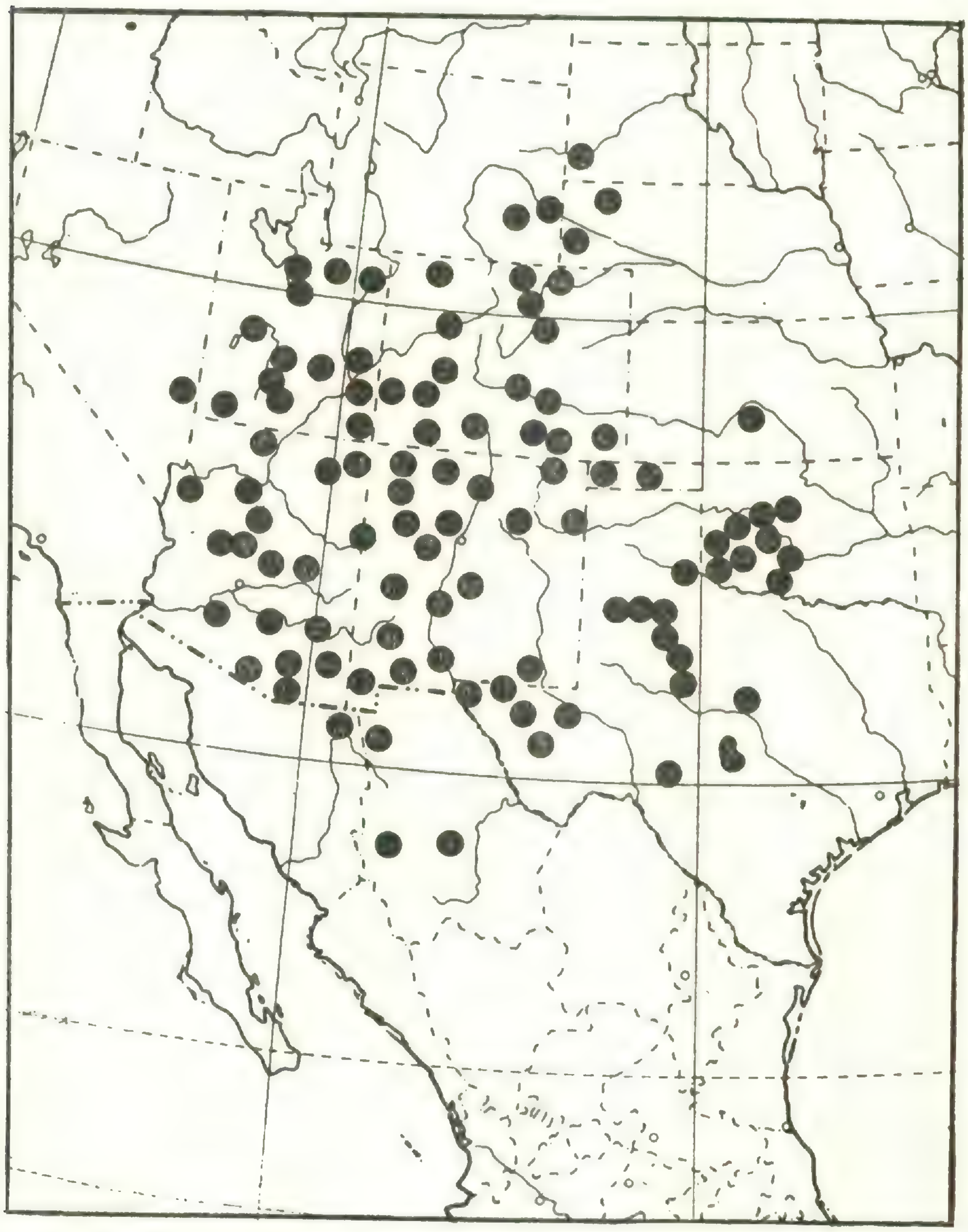
This subspecies is most often confused with ssp. *aurea*. The two are best distinguished by the more strongly monopodial growth form, stouter racemes, generally larger flowers and longer spurs, and, most important, the stouter, more strongly curved, erect or semi-erect fruits of ssp. *occidentalis*. In southwestern United States ssp. *occidentalis* is found at lower elevations as a general rule, but since the seeds of ssp. *aurea* often are washed down from the mountains the latter also sometimes is found at low elevations. The difference between the two represents a summation of several divergent tendencies which together form a rather reliable index to the proper disposition of any given specimen. At the same time the two are segments of a fundamentally heterogeneous species and true intermediates do exist.

Gray referred to this entity in the fifth edition of his 'Manual' but made no clear choice between the two names suggested by Engelmann, *C. aurea* var. *occidentalis* and *C. montana*, as he was undecided whether the plant represented a new species or variety. In 1866 Engelmann, in a letter to Gray (still preserved at the Gray Herb.), made the following statement: "If you retain *montana* as a species you must keep the name, I suppose, but as a variety of *aurea* the name of *occidentalis* is preferable . . .". In 1886, concluding that the entity was truly a variety of *C. aurea*, Gray accepted the name *occidentalis* and published *C. montana* as a synonym. In accordance with this point of view, there seems to be no doubt that the name *occidentalis* should be retained in its modified rank of subspecies.

The specimens cited by Gray in 1886 are of historical interest. Fendler's 1847 collections from Santa Fe, New Mexico, are cited first. These specimens appear to me to be typical but depauperate *C. aurea* ssp. *aurea*. The fact that they were first cited has led to their general acceptance as the historical type of *C. aurea* var. *occidentalis*. The second collection cited is *Wright 1309* from El Paso, Texas, which Gray said is better representative of the entity. This is quite true, and this collection is typical of the subspecies as understood today. Next cited is *Pringle*

198 (later taken as the type of *C. chihuahuana* Fedde) which is again typical ssp. *occidentalis* as are Palmer's 1865 collections from Arizona (at least as to *Coues & Palmer 294*), and *Rusby 9* from the Burrow Mountains. The portion of *Hall & Harbour 31*, cited last, deposited in the Gray Herbarium, is true ssp. *occidentalis;* material bearing identical labels deposited in the Missouri Botanical Garden Herbarium and in the United States National Herbarium is ssp. *aurea.*

Loose, often sandy, dry soil, bottom-lands, prairies, plains, foothills and mesas, and



Map 12. Distribution of *Corydalis aurea* Willd. ssp. *occidentalis* (Engelm.) Ownbey.

along ditches, railroad embankments and washes, at elevations of about 1000–6500 feet; southwestern South Dakota and eastern Wyoming to western Oklahoma, Texas, northern Mexico, and Nevada. Flowers in spring at lower elevations, in summer at higher elevations, from about March 15 to July 30; fruits from about April 1 to August 15.

SOUTH DAKOTA: Fall River County.

NEBRASKA: Banner and Dawes counties.

KANSAS: Stafford County.

OKLAHOMA: Beckham, Blaine, Caddo, Canadian, Cimarron, Custer, Grady, Greer, Jackson, Jefferson, Kingfisher, Kiowa, Texas, and Tillman counties.

TEXAS: Childress, Comanche, Crosby, Culberson, Dickens, Fisher, Hall, Hudspeth, Jeff Davis, Kent, Lubbock, Nolan, Reeves, Scurry, and Sutton counties.

WYOMING: Albany and Platte counties.

COLORADO: Arapahoe, Archuleta, Baca, Boulder, Denver, Fremont, Garfield, Gunnison, Huerfano, La Plata, Larimer, Las Animas, Moffat, Montrose, Ouray, Pueblo, Rio Grande, and Weld counties.

UTAH: Duchesne, Emery, Garfield, Grand, Millard, Piute, Salt Lake, San Juan, Sevier, Uintah, Utah, and Washington counties.

NEVADA: Lincoln County.

ARIZONA: Apache, Cochise, Coconino, Gila, Graham, Maricopa, Mohave, Navajo, Pima, Pinal, Santa Cruz, and Yavapai counties.

NEW MEXICO: Catron, Colfax, Dona Ana, Eddy, Grant, Hidalgo, Luna, McKinley, Quay, Rio Arriba, Sandoval, San Juan, San Miguel, Socorro, Taos, Torrance, and Valencia counties.

CHIHUAHUA: Sept., 1934, *Dobie 13* (UT); Casas Grandes, June 2, 1899, *Goldman 433* (G, US); St. Diego, 6000 ft. alt., April 18, 1891, *Hartman 600* (NY, G, US); Chihuahua, spring, 1936, *LeSueur Mex-516* (UT); Majalca, June 24, 1936, *LeSueur 1207* (M, G); vicinity of Chihuahua, about 4250 ft. alt., April 8–27, 1908, *Palmer 4* (M, NY, G, US); valley near Chihuahua, March 22, 1885, *Pringle 198* (UC, NY, G, US—Isotypes of *C. chihuahuana* Fedde); 14 mi. s. e. of Minaca, 6500 ft. alt., July 25, 1937, *Shreve 8012* (UA); near Colonia Garcia in the Sierra Madres, 7300 ft. alt., July 25, 1889, *Townsend & Barber 163* (M, UC, NMA, NY, G, US—Isotypes of *C. crassipedicellata* Fedde); Santa Eulalia plains, 1885, *Wilkinson* (D).

DURANGO: San Ramon, April 21 to May 18, 1906, *Palmer 72* (M, UC, NY, G, US); Otinapa, July 25 to Aug. 5, 1906, *Palmer 399* (M, NY, G, US).

SINALOA: By spring water in shady canyon, near Platano, Sierra Monterey, March 9, 1940, *Gentry 5869* (M, UA, NY, G).

SONORA: Babispe, 5330 ft. alt., Dec. 24, 1890, *Hartman 358* (G); no definite locality, 1890, *Lloyd 369* (G).

STATE UNCERTAIN: Mexico, no date, *Coulter 664* (M, NY, G).

10. C. PSEUDOMICRANTHA Fedde, Rep. Spec. Nov. **11**:499. 1913 .

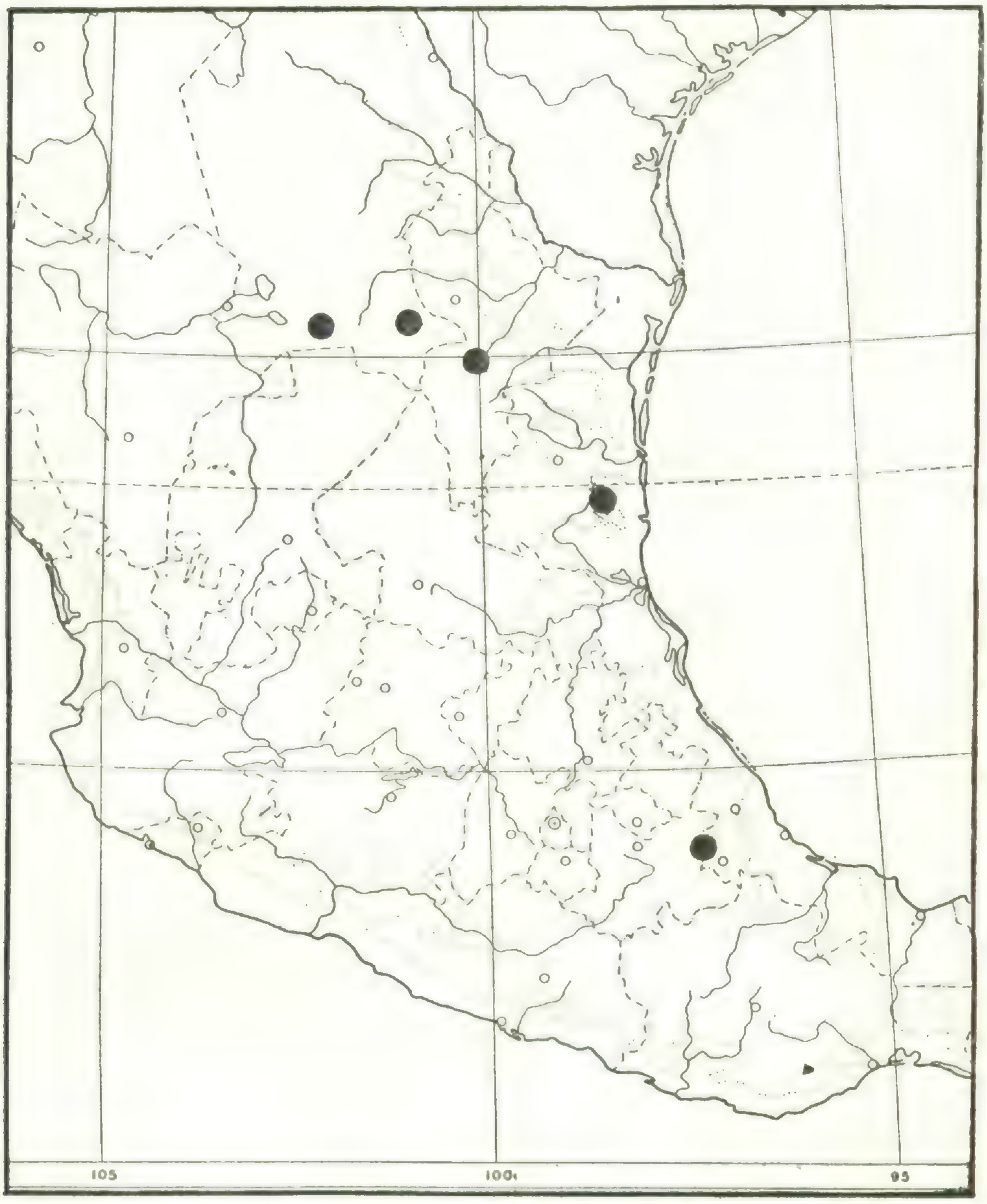
Glaucous or green biennial (or annual?); stems 1–several, sympodial, usually 20–40 cm. long, prostrate-ascending; basal leaves crowded, long-petioled; cauline leaves short-petioled, hardly reduced upward; leaf blades pinnate, the primary segments pinnatifid and again incised, the ultimate lobes elliptical, subapiculate; normal-flowered racemes, when present, 6- to 12-flowered; cleistogamous-flowered racemes abundant, 1- to 5-flowered; bracts elliptical to obovate, 2–8 mm. long, 1–5 mm. broad, often minute on cleistogamous-flowered racemes; pedicels erect, the lower 1–3 mm. long, shorter upward; sepals about 1 mm. long and 0.5 mm. broad, ovate-attenuate; flowers pale yellow, inconspicuous, crowded at anthesis; spurred petal 10–12 mm. long, the hood crestless, the wing margin narrow, the spur 3–4 mm. long, not globose at the tip; spurless outer petal 8–9 mm. long, slender, usually straight; inner petals 7–8 mm. long, narrowly oblanceolate, the

claw about two-fifths the total length; stigma 2-lobed, rectangular, twice as broad as high; fruits erect, commonly 25–30 mm. long, slender, straight or moderately curved; seeds about 2 mm. in diameter, black, submuricately decorated under magnification especially at the often distinct ring margin.

This subspecies is best distinguished by its slender, erect and usually straight fruits, in contrast to those of *C. aurea* ssp. *aurea* which are mostly pendent and curved. The presence of cleistogamous flowers suggests an affinity with *C. micrantha* but size and decoration of the seeds indicate that it is more properly maintained as a distinct species.

Mountains of southern Coahuila to Vera Cruz, Mexico, at elevations of about 7000–9500 feet. Flowers and fruits throughout the spring and summer months.

COAHUILA: Saltillo, Sept., 1898, *Palmer 356* (G, US); Sierra de Parras, 8000–9000 ft. alt., July, 1910, *Purpus 4602* (M, UC, G, US, TYPE).



Map 13. Distribution of *Corydalis pseudomicrantha* Fedde.

NUEVO LEON: Sierra Madre Oriental; lower San Francisco Canyon, about 15 mi. s. w. of Galena, 7500–8000 ft. alt., June 12, 1934, *Mueller & Mueller 773* (UT, G).
TAMAULIPAS: Canyon de Garrapata, April, 1926, *Runyon 1021* (G, US).
VERA CRUZ: Boco del Monte, Aug., 1908, *Purpus 3073* (M, UC, NY, G, US).

INTRODUCED SPECIES

C. lutea DC, a European species, was collected at Elk Rock, Multnomah County, Oregon, *M. W. Gormon 4076,* June 2, 1917 (WS, D); *J. C. Nelson & M. W. Gormon 1259,* same date (G). Gormon made the following comment on the label: "Com. Probably esc. from cultivation. Native of S. Eur. where it runs wild as a weed." This apparently is the only recorded instance of a native European or Asiatic species having escaped from cultivation in the United States. Doubtless it has happened other times, as many Eurasian species are attractive horticultural curiosities and have been grown in this country. Sporadic occurrence of such species or of weedy species accidentally introduced is to be expected.

C. lutea has the following characteristics: Leaves thrice ternately compound or incised, the ultimate segments elliptical; flowers yellow, the spur about one-fourth the total length of the spurred petal; fruit about 10 mm. in length, long-pedicellate.

EXCLUDED SPECIES

Corydalis biaurita Hornem. Hort. Hafn. **2**:668. 1815 = DICENTRA sp.

C. bracteosa Spreng, Syst. Veg. ed. 16. **3**:162. 1826 = DICENTRA sp.

C. canadensis Goldie, in Edinb. Phil. Jour. **6**:329. 1822 = DICENTRA CANADENSIS (Goldie) Walp.

C. Cucullaria Pers. Syn. Pl. **2**:269. 1807 = DICENTRA CUCULLARIA (L.) Bernh.

C. eximia Link, Enum. Hort. Berol. **2**:218. 1822 = DICENTRA EXIMIA (Ker) Torr.

C. formosa Pursh, Fl. Am. Sept. **2**:462. 1816 = DICENTRA FORMOSA (Andr.) DC.

C. fungosa Vent. Choix de Pl. *t. 19.* 1803 = ADLUMIA FUNGOSA (Ait.) Greene.

C. ochotensis Turcz. Reported from Sitka, Alaska, by Regel, in Bull. Soc. Mosc. **34**[3]:142. 1861. This species actually does not occur in America.

C. paeoniaefolia Pers. Syn. Pl. **2**:269. 1807. Listed as a questionable synonym of *C. Scouleri* Hook., Torrey and Gray, Fl. N. Am. **1**:69. 1838. This Asiatic species actually is not found in America.

C. tenuifolia Pursh, Fl. Am. Sept. **2**:462. 1816 = DICENTRA sp.

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The collector's numbers are printed in *italics*, or if the collection is unnumbered, it is indicated by a dash following the collector's name. The numbers in parentheses are those assigned to the species and subspecies in this revision.

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Adams, J. W., & E. T. Wherry. *4698, 4748* (5).
Alexander, A. M. *549a, 549b, 549c* (9).
Allard, H. A. *832, 7895* (4); *232, 2562, 6612, 7620, 7620a, 7630* (5).

Allen, O. D. *118, 311a* (1).
Ames, Mrs. M. E. P. — (2).
Anderson, D., Rhinehart, & Nelson. *849* (9a).
Anderson, E., & D. M. Anderson. *26039* (4).
Anderson, F. W. *274* (9).
Anderson, J. P., & G. W. Gasser. *7320* (4).
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Anderson, W. A. *400* (5).
Anect, Bro. *51, 167* (9).
Applegate, E. I. *8517, 8610* (9); *8450* (9a).
Armstrong, M. *515* (1).
Arsène, Bro. G., & Bro. A. Benedict. *15144* (9).
Arthur, J. C. — (7).
Artz, L. *523* (4).
Ashe, W. W. — (4).
Austin, Mrs. R. M. —, *557, 1393* (2); — (9).
Averill, H. — (4).

Bacigalupi, R. *1628* (2); *2146* (4); *978* (9).
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Baker, C. F. *258, 339, 716* (2a); — (4); *349, 517* (9); *183, 338, 340* (9a).
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Brass, L. J. *14175* (9a).
Braun, E. L. — (5).
Bray, W. L. — (7a); *75* (8).
Breitung, A. J. —, *577* (9).
Briggs, F. P. *1458* (4).
Brigham, Mrs. R. H. *13730* (9).
Bright, J. *14931* (4); *14281, 14283* (5).
Brinkman, A. H. *4436* (4); *2015, 4114a, 5253* (9).
Britton, N. L. — (5).
Britton, N. L., E. G. Britton, & A. M. Vail. — (4).
Broadhead, G. C. — (6); — (7).
Brooks, H. E. — (4).
Brown, A. H. *37* (6).
Brown, S. *62, 214* (9).
Bruce, Mrs. C. C. —, *1192* (2); *2206* (9).
Bruhin, T. A. — (7).
Bryan, W. C. *74* (9).
Bryant, Mrs. — (3).

Buffum, B. C. *51* (9).
Bull, R. — (9a).
Burgess, T. I. W. — (4).
Burnham, S. H. — (4).
Bush, B. F. —, *1*, *22*, *63*, *1386*, *4375*, *7445*, *7914*, *13237*, *13237A*, *13259*, *13259A*, *13280A*, *14400*, *14403*, *14408*, *14460*, *14480*, *14525*, *14543* (5); *523*, *1295*, *1610*, *5615*, *5615A* (6); *8*, *22*, *23*, *71*, *617*, *887*, *1081*, *1328*, *1649*, *4369*, *4925*, *5519*, *7109*, *7440*, *7568*, *7568A*, *10409*, *13280*, *13459*, *14461*, *14481*, *14498* (7); *4*, *19*, *317*, *519*, *1014*, *1120*, *1345*, *1377*, *14578*, *14606*, *14629* (7a); *1209* (8); *575* (8a).
Butler, G. D. *12*, *41*, *10975* (6); — (7).
Butters, F. K., & M. F. Buell. *349* (4); *419* (9).
Butters, F. K., & C. O. Rosendahl. *1342* (9).

Cain, S. A. *56* (9).
Cameron, C. *53* (9a).
Camp, W. H. *1285* (4); *1333* (5).
Canby, W. M. — (4); — (5).
Cantelow, Mrs. H. C. — (2).
Carberry, C. *43* (6).
Carleton, M. A. *35* (6); *49* (7a).
Carr, L. G. *911* (4).
Carr, W. P. *125* (9).
Carrasco, L. — (8).
Carter, M. R. *23* (9).
Carter, W. R. — (1).
Case, E. L., & J. G. Lemmon. — (2).
Castetter, E. F. *1142*, *1403* (9); *1416*, *1436*, *1482* (9a).
Chamberlain, E. B., & C. H. Knowlton. — (4).
Chamberlin, Myrtie. *12* (7).
Chandler, A. *2127* (7).
Chaney, R. W. *151* (4).
Chapman, A. W. — (4); —, *65* (7a).
Chapman, J. W. *28* (3).
Chapman, Mrs. J. W. *1* (3).
Charette, L. A. *254* (4).
Chase, A. *2173* (5).
Chase, V. H. *5159* (5); *3822* (7).
Child, M. *562* (9a).
Churchill, J. R. — (4); — (5); —, *418* (7a); — (9).
Clark, H. S. — (5).
Clark, O. M. *8412* (9).
Clark & Devitt. *10* (6).
Clausen, R. T., & E. R. Clausen. *5702* (5).
Clausen, R. T., & H. Trapido. *2813* (9).
Clemens, Mrs. J. *11589* (7).
Clemens, J., & Mrs. J. Clemens. *797* (8).
Clements, F. E., & E. S. Clements. *110*, *257* (9).
Cleveland, D. — (2).
Clokey, I. W. *2740*, *7096*, *7522*, *7928* (9); *2771* (9a).
Clover, E. U. *6354* (9a).
Cockerell, T. D. A. — (9).
Cockerell, T. D. A., & M. D. Cockerell. *32* (9a).
Cocks, R. S. — (7a).
Coghill, G. E. *95* (9).
Cole, L. A. *103* (4).
Collier, A. J. — (3); *72* (4); *73* (9).
Collins, J. F., & M. L. Fernald. *85* (9).
Collom, Mrs. R. E. *140*, *143* (9).
Commons, A. — (5).
Conard, H. S. *150* (1).
Constance, L., & F. W. Pennell. *2022* (2d).
Cooke, W. B. *14041* (5).
Coombes, Mrs. A. L. — (2).
Cooper, Dr. — (1).
Cooper, W. S. *24* (4); *11*, *188* (9).
Copeland, E. B. — (2).
Copeland, H. F. *203*, *758* (2).
Core, E. L. —, *2886* (4).
Correll, D. *107* (4).
Cory, V. L. *291*, *38687* (8); *5447*, *13662* (9a).
Cottom, W. P. *4773*, *5917* (9).
Coues, E., & E. Palmer. *294* (9a).
Coulter, T. *664* (9a).
Coville, F. V. — (4); — (9).
Coville, F. V., & T. H. Kearney. *1810*, *1966*, *2033* (3).
Cowen, J. H. *39*, *629* (2a); *30* (9); *38*, *476a* (9a).
Cowles, H. C. *629* (1).
Crandall, C. S. *1244* (4); *28*, *238*, *470* (9); *236*, *238*, *473* (9a).
Crandall, C. S., & J. H. Cowen. *35* (9).
Cratty, R. I. — (7).
Cronquist, A. *2854* (2c); *1414*, *1415*, *2724*, *2834*, *3158*, *3323* (9); *895* (9a).
Curtis, L. B. — (7).
Curtiss, A. H. —, *11* (5); —, N. Am. Pl. *125* & *125a*, *4208*, *4515*, *4516* (7a).
Cusick, W. C. —, *190*, *354*, *1728*, *2431*, *2431a* (2c).
Cutler, H. C. *771*, *4638* (9a).

Dale, E. E. Jr. *43* (9).
Damon, W. E. *67* (4).
Daniels, F. *82* (9a).
Darlington, W. — (5).
Davis, J. —, *73*, *1435*, *3833*, *4415*, *4415a*, *6363*, *6387* (5); *1211* (7).
Davis, R. J. *2746* (2c); *275-37* (2d).

Deam, C. C. *31641* (4); —, *12574* (5).
Degener, O. *4841* (9a).
Degener, O., & L. Peiler. *16790* (9).
Demaree, D. *4732, 10594, 12059* (5); *3039, 12111, 15095, 20884, 20885, 20920, 22023* (6); *14516, 20870* (7a); *11898, 12351, 12547* (8a); *7470, 12193* (9a).
Dewey, L. H. *1* (4); *225* (5).
Dixon, J. *17, 25* (3); *45* (4).
Dobie, Mrs. B. McK. *13* (9a).
Dodge, C. K. *43* (5); *1* (9).
Dougan, L. M. — (7).
Downey, J. *1818* (9).
Doyel, Mrs. — (7).
Drouet, F. — (6); *364* (7).
Drummond, T. *16* (7a).
Drushel, J. A. *1387* (4); —, *4059, 4094* (5); *1819* (9).
Duran, V. *3069* (9).
Dutton, D. L. — (4); — (9).
Dwight, N. E. *9* (9a).

Ealy, R. *20* (6).
Eames, A. J., & L. H. MacDaniels. *2366, 2367* (9).
Earle, F. S. *503, 503a, 643* (9); — (9a).
Earle, F. S., & S. M. Tracy. *135, 392* (8).
Earle, R. E. — (4).
Eastwood, A. *1758* (2); — (2a); *307, 380* (3); *133* (9); *6093, 8204* (9a).
Eaton, D. C. — (7a).
Eaton, D. W. — (3).
Eby, A. F. — (4); — (5); — (9).
Eby, J. H. — (4); — (9a).
Edie, M. C. *2* (9).
Edmonds, H. W. — (4).
Edmondson, T. W. *1106, 4995* (4).
Edwards, O. T. — (1).
Eggert, H. — (5); — (7); — (7a); — (7b); *106* (8a).
Eggleston, W. W. *5656* (2a); *3015* (4); *10439, 11955, 18674, 20251* (9); *6402, 6427, 6447, 14322, 19825, 19982* (9a).
Eggleston, W. W., & M. L. Fernald. — (4).
Ehlers, J. H. *252, 6208* (4); —, *7558* (9).
Ellis, C. C. *6* (9).
Elmer, A. D. E. —, *1018* (9).
Elmore, F. H. *8* (9a).
Elrod, M. J. *51* (9).
Emerton, J. H. — (4); — (9).
Emig, W. H. *520* (7).
Engelmann, G. — (1); — (4); — (5); —, *132* (6); — (7); — (9).
Engelmann, H. — (9a).
Engleman, J. *1569, 1571* (7); *213, 1570, 1572* (8a); *1566, 1567, 1568, 1695* (9a).
Epling, C. *6371* (1); *5842* (7).
Epling, C., & J. M. Houck. *9358* (2d).
Epling, C., & W. Robison. — (2).
Eskew, C. T. *1557* (7); *1585* (8a); *203, 243* (9).
Evans, W. J. *43* (6).
Eyles, D. E. *7725* (5).

Fassett, N. C. *3853* (4); *20937* (5); *20113* (7).
Fassett, N. C., & W. C. Meyer. *5717* (7).
Faxon, C. E. — (7a).
Faxon, E., & C. E. Faxon. — (9).
Fendler, A. *17* (9).
Fendler, F. S. *1445* (4).
Fernald, M. L. — (4).
Fernald, M. L., & J. F. Collins. *1050* (9).
Fernald, M. L., & H. B. Jackson. *12098* (4).
Fernald, M. L., & J. B. Lewis. *14536* (5).
Fernald, M. L., & B. Long. *23865, 23866* (4); *7041, 11838, 12083* (5).
Fernald, M. L., B. Long, & E. C. Abbe. *14157* (5).
Fernald, M. L., B. Long, & A. S. Pease. *11685, 11686, 11687* (5).
Fernald, M. L., & A. S. Pease. *25088* (4).
Fernald, M. L., & H. St. John. *7502* (5).
Fernald, M. L., & W. C. Strong. *429* (4).
Fernald, M. L., & K. M. Wiegand. *5455, 5456* (4).
Fernald, M. L., K. M. Wiegand, & A. J. Eames. *14295* (4).
Ferris, R. S., & R. Duthie. *1002* (2c); *1068* (9).
Fiero, K. *23* (9).
Fiker, C. B. *1674* (9).
Fink, B. — (7).
Fisher, G. L. — (7a).
Fisher, H. L. — (4).
Fitzpatrick, T. J., & M. F. L. Fitzpatrick. *1* (7).
Flint, M. B. — (5).
Flodman, J. H. *486* (9).
Fogg, J. M. Jr. *4984, 13459, 14552, 15115,* (4); *1579* (5).
Fordwood, W. H. *139, 365* (9).
Foster, R. C., & J. F. Arnold. *199* (9a).
Fowler, J. — (4); — (9).
Freeborn, R. *338* (7b).
Freeman, O. M. — (4); — (7a).
French, G. H. — (5).
Friesner, R. C. *2726, 8528, 16649* (5).
Frye, W. M. — (4).
Fuller, T. O. — (7a).
Fulton, H. J. *7165* (9a).

Galway, D. *8415* (9a).
Garrett, A. O. *5498*, *8453* (9); *2555* (9a).
Garvin. — (9a).
Gary, L. B. *575* (5).
Gates, F. C. *12453* (4); *10205* (5).
Gates, F. C., & M. T. Gates. *10368* (4).
Gayle, E. E. — (7).
Gentry, H. S. *5869* (9a).
Geyer, A. — (5).
Gilbert, F. A. *43* (5).
Gilbert, F. A., L. O. Williams, & C. Smithson. *404* (5).
Gilbert, G. — (4).
Gilbert, J., & T. Gilbert. — (4).
Gilman, M. F. *47* (9a).
Girard. — (8).
Glatfelter, N. M. — (4); —, *61* (5).
Gleason, H. A. *9723* (4); — (5).
Glismann, D. *42* (9a).
Goddard, P. E. *489* (9).
Godfrey, R. K., & R. N. White. *7054* (7a).
Goldman, E. A. *433* (9a).
Goodale, A. S. *69962* (7a).
Goodding, C. O. *6429* (9).
Goodding, L. N. *69*, *69a*, *1027*, *1189*, *1223*, *1315*, *1501*, *2071* (9); *931* (9a).
Goodman, G. J. *2533* (6).
Goodman, G. J., & C. L. Hitchcock. *1205*, *1484* (9).
Goodman, G. J., & L. B. Payson. *2840* (9a).
Gorman, M. W. *1023* (9).
Gould, L. — (7a).
Grace, M. C. *152* (8a).
Graham, E. H. *3771*, *8635*, *9287* (9); *7882*, *8014* (9a).
Grant, A. L. *1645* (5).
Grant, G. B. *132*, *2726* (9).
Grant, J. M. —, *7936* (1).
Grant, M. L. *2845* (4); *2846* (9).
Grassl, C. O. *3766* (4).
Graves, E. W. —, *1757* (7).
Gray, A. — (9); — (9a).
Gray, F. W. *5134* (4).
Greenman, J. M. *235*, *236*, *238*, *372* (4); *3958*, *4212* (5); *2184*, *3392* (9).
Greenman, J. M., O. E. Lansing Jr., & R. A. Dixon. *132* (4).
Griffith, H. R. *35* (5).
Griffiths, D. — (9); *2280*, *2379*, *2648*, *3553*, *3846*, *4176* (9a).
Griscom, L. — (4).
Grout, A. J. — (4).

Haberer, J. V. *55* (4).
Hale, J. — (7a).
Hall, D. *8415*, *8506* (9a).
Hall, E. — (7); *11* (7a).
Hall, E., & J. P. Harbour. *31* (9, 9a).
Hall, H. M. *9308*, *9796* (2).
Hall, H. M., & E. B. Babcock. *4291* (2).
Hamilton, L. P. — (9a).
Hanna, G. D. — (3).
Hanson, H. C. —, *364* (8); *A108*, *C363* (9a).
Hanson, H. C., & E. E. Hanson. *A1179*, *A1180* (9a).
Hardin, E. — (9).
Harper, D. C. — (2a); — (9).
Harper, F. *53* (4).
Harper, R. A. — (4).
Harper, R. M. *3296* (5); *10* (6).
Harper, R. M., & H. Kurz. — (7a).
Harrington, G. L. *57* (3).
Harrington, H. D. *1621* (2a); *3* (9).
Harris, M. *3605* (9).
Harrison, B. F. *113*, *6158*, *7471*, *9163*, *10165* (9); *6399*, *9630*, *10155* (9a).
Harrison, G. J. *7894* (9).
Harrison, J. J. — (7b).
Hartman, C. V. *358*, *600* (9a).
Harvey, F. L. —, *1*, *4*, *16*, *125** (6); — (7).
Harvey, F. L., & L. H. Harvey. — (4).
Hasse, H. E. — (7a).
Hastings, G. T. — (4).
Havard, V. — (7a); — (8); — (9a).
Hayden, A. *5045*, *5047*, *5056*, *11246*, *11247* (7).
Hayden, F. V. — (5); — (7); *56* (9); — (9a).
Hawk, H. A. — (6).
Hayward, H. E. *638*, *645*, *1335* (9).
Heald & Wolf. *711* (8).
Heath, H. — (3).
Hedrick, D. C. *252* (8).
Heideman, C. W. H. *66* (9).
Heidenreich, V. T. *193* (9).
Heller, A. A. *12047*, *14685*, *16284* (2); —, *9* (4); —, (5); *1433* (7a).
Heller, A. A., & E. G. Halbach. *1209* (4).
Heller, A. A., & E. G. Heller. *3871* (1); *3500*, *3529* (9); *3515* (9a).
Henderson, J. B. *33*, *5689* (6).
Henderson, L. F. *49*, *546 of 1924* (1); *3265* (2c); *3716* (9).
Hermann, F. J. *7290*, *7529*, *7748*, *8729* (4); *10087* (7a); *5247*, *7749* (9).
Herrick, C. L. *259*, *524*, *1006* (9).
Herriot, W. — (9).
Hershey, A. L. *3971*, *3972*, *3974*, *3978*, *3980* (9); *3973*, *3975*, *3976*, *3977*, *3979* (9a).
Hexamer, F. M. — (4).

Hicks, G. H. — (4).
High, M. M. *91* (7b).
Hildebrand, Mrs. W. J. *21007* (7a).
Hill, G. A. *65* (3).
Hills, F. G. — (4).
Hinckley, L. C. *2893* (8); *217* (9).
Hitchcock, A. E. *1119, 1287* (9).
Hitchcock, A. S. — (4); *1040* (5); *1039* (6); *32, 1041* (7); *1038* (8a); —, *12042, 12064* (9).
Hitchcock, C. H. — (9).
Hitchcock, C. L. *2317* (9).
Hitchcock, C. L., & J. S. Martin. *7412, 7485* (9).
Hitchcock, C. L., & C. V. Muhlick. *8713, 9747, 10216* (2c); *9370, 11568, 12138* (9).
Hogin, L. — (8).
Holman, P. — (4).
Holmgren, A. H. *875, 1113, 1973* (9); *3279* (9a).
Holmgren, A. H., & S. Hansen. *3509* (9).
Holzinger, J. M. — (7); —, *33* (9).
Hooker, J. D., & A. Gray. — (2b).
Hope, C. *9340* (9a).
Hopkins, M. *1664* (6); *1416, 3089* (8a); *1374* (9a).
Hopkins, M., & G. L. Cross. *1549* (5); *1774* (6).
Hopkins, M., E. R. MacDowell, & M. P. Copeland. *6394* (7).
Hopkins, M., A. Nelson, & R. A. Nelson. *206, 233* (8a); *267* (9a).
Horne, W. T. — (3).
Hosie, R. C., S. T. Losee, & M. W. Bannan. *1411, 1412* (4); *1413* (9).
House, H. D. *3651, 5153, 16214, 24625, 28184* (4); *3228* (7a).
Howell, J., & T. J. Howell. — (1).
Howell, T. J. —, *31*, (1); — (9).
Hudson, Bonnie L. *124* (5).
Huett, J. W. — (7).
Hughes, E. L. *44* (9).

Ifft, J. *34* (1).
Innes, R. R. *614* (7a); *340* (8).
Innes, R. R., & B. H. Warnock. *423, 472* (8).

Jaussan, K. P. — (4).
Jeff & Watts. — (9a).
Jennings, O. E. — (5).
Jennison, H. M. *716* (5).
Jermy, G. — (7a); —, *203* (8).
Joeger, H. F. — (9).
Johnson, P. *276* (9).
Johnston, E. L. *21* (9); *1121* (9a).
Johnston, E. L., & G. G. Hedgecock. *820* (9a).
Jones, G. N. —, *8794* (1); *5068, 6961, 6962, 6963* (2c); *5405* (9).
Jones, I. *67* (4).
Jones, M. E. — (2); —, *1197* (2b); *20365* (7b); *85, 5085, 5486a, 5684j* (9); —, *5183b, 5196, 5196c, 5249a, 5315a, 5350, 6002b, 25760* (9a).
Joor, J. F. — (7a).

Kaye, D. *1501* (4).
Kearney, T. H. *123, 301* (4).
Kearney, T. H., & R. H. Peebles. *9237, 11251* (9).
Keck, D. D. *641* (9).
Keefe, A. M. — (4).
Keesecker, B. P. *12* (6).
Keever, C. *412* (4).
Kellogg, J. H. — (4); —, *76, 281, 916* (5); — (6); — (7).
Kennedy, G. G. — (4).
Kennedy, P. B. *4488* (9).
Kennicott, R. — (4).
Ketchum, F. E. — (9).
Killian, O. L. —, *6954* (7a).
Killip, E. P. *36503* (9); *36489* (9a).
Kincaid, T. — (1); — (3).
Kirkwood, J. E. *1712* (2d); *2454* (9).
Kirkwood, J. E., & J. W. Severy. *1712* (2d).
Knight, W. C. *50* (7).
Knowlton, C. H. — (4).
Knowlton, F. H. — (5); *6* (9).
Kriebel, R. M. *3105* (5).
Krotkov, P. V. *7459, 9063* (9).

Laing, H. M. *174* (4).
Lakela, Olga. *1300, 2461, 2485* (4); *2403, 2926* (9).
Lamb, F. H. *1063* (1).
Lane, W. C. — (4).
Langford, T. E. — (9).
Langlois, A. B. — (7a).
Lappin, A. F. *84* (9); *85* (9a).
Large, J. W., & R. T. Clausen. *1264* (4).
Lea, M. C. — (4).
Leding, Mrs. *1119* (9).
Lee, F. S. — (7a).
Leggett, W. H. — (5).
Leiberg, J. B. *5184* (2); *1190* (2d); *473, 564* (9); *5503* (9a).
Lemmon, J. G. —, *9, 16* (2).
Leonard, F. E. — (2b).
LeSueur, H. *Mex-516, 1207* (9a).
Letterman, G. W. —(5); — (7); — (9).
Lewton, F. L. *45* (7a).
Lighthipe, L. H. *198, 651* (7a).

Lighthipe, M. L. — (4).
Lindheimer, F. L. —, *433, 546, 663* (8).
Lindsay, A. A. *4556* (1).
Little, C. S. *1* (9).
Little, E. L. Jr. *54, 1023* (5); *123, 651, 1022, 1024* (6); *534* (9a).
Little, Mrs. E. L. *1021* (5); *1020* (7a).
Little, E. L., & Mrs. E. L. Little. *119* (5).
Livingston, G. A. *47* (2a).
Livingston, R. B. *175, 301* (9).
Lloyd, C. E. *369* (9a).
Lloyd, C. G. — (5).
Lloyd, F. E. — (1); — (4).
Lodewyks, M. C. *87* (7).
Loest, E. — (8a).
Long, B. *50047* (4); *42948, 56265* (5).
Loomis, H. F. *926* (9a).
Lucas, W. D. *242, 245* (9).
Lucas, W. D., J. T. Painter, & F. A. Barkley. *14236* (8).
Luckhardt, R. *185* (7).
Lunell, J. — (9).

McAtee, W. L. *3227* (4); *3451* (7a).
McBryde, J. B. — (7a); *M1007* (8a).
McCalla, W. C. *2124* (9).
McCart, W. L. *985* (6); *1569-2* (8a).
McCauley, Lt. — (2a).
McClellan, B. *10* (7).
McClellan, J. T. *12* (7).
McCree, J. *633* (5).
McCubbin. — (5).
McDonald, F. E. — (7).
McFarland, F. T. *22* (4).
McIntosh, A. C. *138* (9a).
McKelvey, S. D. *1686* (7a); *2000* (8); *2402, 4802* (9); *4330, 4438* (9a).
McLean, D. *27* (6).
McMullen, E. — (6).
McMurry, F. B. *655* (8a).
McVaugh, R. *4950* (4); *4906* (5).
Macbride, J. F. *595* (2c).
Macbride, J. F., & E. B. Payson. *3287, 3457* (9).
MacDougal, D. T. *250* (9); *83, 105, 114* (9a).
Macfadden, F. A. *15514* (2c).
MacIntyre, Mrs. — (3).
Mackaness, F. — (4).
Mackenzie, K. K. *677, 2612* (4); —, *5756* (5); —, *17, 25, 33, 50* (7); *58* (9).
MacLean, J. — (4); — (9).
Macoun. —, *99* (4); *7, 112* (5); —, *100* (9).
Macoun, J. M. — (3); — (4); — (9).
Macoun, John. — (4); — (5); — (9).
Macoun, John, & W. Herriot. — (9).
Maguire, B. *861a, 3460* (9).
Maguire, B., & H. L. Blood. *1364, 1863* (9a).
Maguire, B., & G. Piranian. *12478* (2a).
Maguire, B., & J. D. Redd. *1862* (9).
Manning, W. H. — (9).
Marcelline, Sister M. *2063* (9).
Marie, P. Louis. — (4).
Marshall, W. F. *475* (9a).
Martin, B. — (7a).
Mason, H. L. — (3); *3423, 3473* (9).
Mason, R. F. *61, 85, 87* (6); — (7).
Massey, A. B. *849* (4); *1749, 3799* (5).
Mathias, M. E. *143* (4); *386, 593* (9).
Maxon, W. R. *75* (5).
Maxon, W. R., & T. R. Robinson. *3* (4).
Maxon, W. R., & P. C. Standley. *253* (5).
Mearns, E. A. — (7); *278, 566, 1045, 1265, 3790, 4968* (9); —, *305* (9a).
Mearns, E. W. *57, 58* (4).
Memminger, E. R. — (4).
Mendenhall, W. C. — (3); — (4).
Mericle, L. *449* (9a).
Merrill, E. D., & E. N. Wilcox. *646* (9).
Mertie, J. B. *60* (3).
Mertz, H. N. — (5).
Metcalfe, O. B., *877, 980* (9); *19, 1050* (9a).
Metz, Sister M. C. *2151* (8).
Mexia, Ynes. *2040* (3); *2106, 2240* (4).
Meyer, F. G. *468, 2159* (1).
Miller, A. — (2c).
Miller, G. S. Jr. *443* (7a).
Miller, W. N. *86* (4).
Milligan, Mrs. J. M. — (6).
Millspaugh, C. F. *446* (4); *14* (5).
Minshall, W. H. *42* (9).
Moffatt, W. S. *353, 413* (4).
Mohr, C. — (5); — (7a).
Moldenke, H. N. *8768* (4); *2455* (5); *1981, 8204* (9).
Moodie, M. E. *137, 911* (9).
Moore, A. H. *1667* (4); *5092* (5).
Moore, E. J. — (9).
Moore, F. L., & C. E. Moore. — (4); — (7); — (9).
Moore, H. E. Jr. *625* (7a).
Moore, J. A., & J. A. Steyermark. *3065, 3664* (9).
Moore, J. W., & B. O. Phinney. *12372* (7).
Moore, J. W., & C. O. Rosendahl. *13351* (9).
Moritmer, M. F. *83* (5).
Morton, M. D. *200* (6).
Moseley, E. L. — (5).

Moss, E. H. *2255* (4); *2140* (9).
Moyer, Dr. — (4).
Mueller, C. H., & M. T. Mueller. *773* (10).
Muenscher, W. C. *42* (4); *15512* (5); *3138* (7).
Muenscher, W. C., & B. Maguire. *2280* (4); *2326* (9).
Muenscher, W. C., W. E. Manning, & B. Maguire. *394* (4).
Muenscher, W. C., & M. W. Muenscher. *14279* (7a).
Muir, J. *168* (3).
Mulford, A. I. — (2c).
Murdock, John Jr. *3022, 3092, 4640* (9).
Murie, O. J. — (4).
Murphey, E. V. A. *65½* (9).
Myers, I. J. *75* (9a).
Myers, J. — (5).

Nash, G. V. *289* (4).
Nease, F. *23* (8a).
Nelson, & D. Anderson. *978* (9).
Nelson, J. Smith, & Merkle. *109* (8a); *103* (9a).
Nelson, A. *10886* (5); *10858* (6); *118, 124, 1241, 1679, 1921, 2395, 3164, 3926, 4027, 4676, 7181, 10501, 11495* (9); *369* (9a).
Nelson, A., & J. F. Macbride. *1833, 2154* (9).
Nelson, A., and E. Nelson. *5684, 6221* (9).
Nelson, A., & R. A. Nelson. *W-2206* (3); —, *W-2151, 2395, 3622, 3833* (4); *5006, 5019* (8); *2103x, 4010* (9); *1395, 1491, 2005, 2005a, 2786* (9a).
Nelson, E. *210* (9).
Nelson, E. W. *4841* (9).
Nelson, J. C. *2569* (1).
Nelson, M. L. *43* (8a).
Nelson, N. L. T. *27* (2a).
Nelson, P. M. *45* (6).
Newcombe, W. A. *10* (9).
Nichol, A. A. — (9).
Noll, H. R. — (4).
Normand, J. F. — (6).
Norton, J. B. *174* (4); *431* (7a); *14, 14a* (7).
Nuttall, L. W. — (5).

Ohlweiler, W. W. — (5).
Olguin, M. — (8).
Onion, I. S., R. Kennicott, & W. L. Hardisty. — (9).
Oosting, H. J. *1787* (4).
Orcutt, C. R. *5829* (7b).
Osborn, B. *1487R* (5); *461R* (8a).
Osborn, W. J., & H. J. Fulton. *7152* (9a).
Osterhout, G. E. —, *782, 1748, 2280, 2281, 2448, 3702, 6984* (9); *1950, 2614* (9a).
Otis, I. C. *1420, 1512* (1).
Over, W. H. *5139* (7); *1753* (9a).
Overholts, L. O. —, *10096* (9).
Ownbey, M. *710* (9).
Ownbey, M., & G. B. Ownbey. *2935, 2938* (2); *3034, 3034a, 3053* (2a); *3057* (2b); *3062, 3064, 3066, 3067, 3071* (2c); *3077, 3089, 3089a* (2d); *1017, 2815, 3016, 3018, 3032, 3035, 3041, 3048, 3050, 3055* (9); *3007* (9a).
Oyster, J. H. — (7, 7a).

Pace, L. *61* (7a); *295* (9).
Painter, J. H. *2* (5).
Painter, J. T., & F. A. Barkley. *14461* (7b).
Painter, J. T., W. D. Lucas, & F. A. Barkley. *14235* (7a).
Palmer, Edward. — (8a); *11* (9); *4, 72, 399, 9902* (9a); *356* (10).
Palmer, E. J. *289, 1616, 1676, 1676A, 5428, 9414, 14758, 24778, 29748, 33202, 33209, 39156, 39996* (5); —, *37, 288, 888, 1738, 1738A, 1702, 3412, 4921, 13428, 24726* (6); *1625, 1645, 1674, 1678, 1702, 1710, 5514, 24594, 24769, 24847* (7); *4827, 7106, 13126, 13146, 13436, 39166* (7a); *9064, 11239* (7b); *11396, 34424* (8); *31188, 31346, 34296, 34335, 34543, 37394, 37398, 37448* (9); *33966* (9a).
Palmer, L. J. *194* (3); *1769* (4); *1750* (9).
Palmer, W. *178* (3).
Palmer, W., & W. H. King. *148* (4).
Pammel, L. H. — (7); *307* (9a).
Pammel, L. H., & E. M. Stanton. *46* (9).
Parish, W. F. *5* (9a).
Parks, H. B. *2202* (7a); *1429, 29500* (7b).
Parry, C. C. — (2).
Patterson, H. N. — (7); *171* (9).
Paxton, B. *117* (6).
Payson, E. B. *1664* (5); *71* (9); *249* (9a).
Payson, E. B., & L. B. Payson. *2799, 4722* (9); *3838* (9a).
Pease, A. S. *606, 10773* (4); *7396, 19016* (5); *18010, 18029* (9).
Pease, A. S., & R. C. Bean. *23549* (4); *23537, 26128, 26393* (9).
Pease, A. S., & E. C. Ogden. *25111, 25161, 25190* (9).
Peck, M. E. *4133, 4136, 9616, 15331, 20946, 21442* (9).

Peebles, R. H., & E. G. Smith. *11555* (9).
Penard, E. *39* (9).
Penfound, W. T. — (5); — (7); — (7a).
Pennell, F. W. *5761* (9a).
Perrin, L. —, *77* (6).
Perry, R. C. — (6).
Phelps, O. P. *490* (4).
Pickett, R. *64* (9).
Piper, C. V. —, *19, 4958* (1); *4057* (2d); —, *2253* (9).
Piper, R. H. *112, 1525* (4).
Plank, E. N. — (6); — (7a).
Pollard, C. L. *48, 136* (5).
Pollock, W. M. — (4).
Polson, M. *19* (6).
Poole, S. F. *121* (7).
Porsild, A. E., & R. T. Porsild. *135, 739* (4).
Porter, C. L. *3045* (9); *2858* (9a).
Poto, W. L. *121* (4); *14* (9).
Preble, A. E., & M. Cary. *13* (4); *5* (9).
Preble, E. A., & G. Mixter. *619* (3); *601, 689b* (9).
Preble, E. A., & A. E. Preble. *91* (4).
Pringle, C. G. —, *198* (9a).
Pulling, H. E. — (4).
Purpus, C. A. *6550* (9); *7058* (9a); *3073, 4602* (10).
Pusonett, K. *59* (7a).

Quarterman, E. *709, 1094* (5).
Quick, C. R. *1072* (2d).

Radford & Stewart. *32* (7a).
Ramaley, F. *1165, 1413* (9).
Ramaley, F., & K. R. Johnson. *14731* (9).
Ramaley, F., & Richards. *15960* (9a).
Ramaley, F., & W. W. Robbins. *2465* (9).
Rand, E. L., & B. L. Robinson. *121* (4).
Randel, W. *21* (7).
Randolph, L. F., & F. R. Randolph. *1143* (4).
Raup, H. M. *2443-a, 6088, 6115, 7624* (4); *2438-a, 2439-a, 2440-a, 2442-a, 6033, 6052* (9).
Raup, H. M., & E. C. Abbe. *4473, 4531, 4595* (4).
Redfield, J. H. —, *287, 288* (4); *279, 280, 281* (5); *283* (9).
Reed, E. L. *1825* (8).
Reed, J. F. — (4).
Reed, J. F., & M. S. Reed. — (7a).
Reppert, F. — (8a).
Reverchon, J. —, *2736, 3711, 4357* (6); *1896* (7); —, *1896, 2735, 2963, 3710* (7a); —, *3707, 3709* (8); — (8a).
Reynolds, H. C. *1419, 2968, 2981, 3059, 3327, 3846* (7).
Rhoades, W. — (4).
Rice, E. *37* (8a).
Ricker, P. L. — (4).
Rickett, H. W. *496* (5); *466* (7).
Riedel, M. — (7a).
Riehl, N. — (7).
Rinehart, F. *210* (7a); *234* (8a).
Robbins, W. W. *4896* (9).
Robinson, B. L. —, *80* (4); *251* (7a).
Robinson, T. R., & W. R. Maxon. *3* (4).
Rodgers, L. *343* (4).
Roland, A. E. *41416* (4).
Rolland, Fr. *7150, 15761* (9).
Rollins, R. C. *2003* (2a); *1963* (9).
Rose, J. N., & J. H. Painter. *8128* (4).
Rose, J. N., W. R. Fitch, & T. H. Parkhurst. *17710* (9).
Rose-Innes, R. *41022* (7a).
Rosendahl, C. O., & F. K. Butters. *1565* (1); *3193* (7).
Rossback, G. B., & R. P. Rossback. *476* (1).
Rothrock, J. T. *22, 28* (9).
Rousseau, J. *25264, 26971* (4); *26401, 26592, 26657, 26871* (9).
Rowlee, W. W., K. M. Wiegand, & G. T. Hastings. — (4).
Runyon, E. *47* (8a, 9a).
Runyon, R. *1618* (7b); *1021* (10).
Rupp. — (5).
Rusby, H. H. *282, 291* (4); *9* (9a).
Russell, C. — (7); — (7a).
Rust, H. J. *621* (9).
Ruth, A. *361* (4); *194, 228, 231, 233, 363, 1674, 1841* (5); *1175* (6); *1053* (7a); *3* (9a).
Rutter, C. —, *92, 179, 206* (3).
Rydberg, P. A. *6848* (2b); *8191, 9239, 9653* (4); *125, 512, 513* (9); *10, 513* (9a).
Rydberg, P. A., & A. O. Garrett. *8873* (9); *9208* (9a).
Rydberg, P. A., & R. Imler. *403* (6).
Rydberg, P. A., & R. K. Vreeland. *6262, 6263* (9); *6261* (9a).

Safford, H. T. — (5).
Safford, P. — (2).
Safford, W. E. *116* (4).
St. John, H. *8662* (1); *6361, 7629* (9).
St. John, H., & B. Long. *1030* (5).
St. John, H., & D. White. *22* (4).
St. John, Mrs. O. — (9a).
Sandberg, J. H. —, *163* (4); —, *18, 434, 1025* (9).

Sandberg, J. H., & J. B. Leiberg. *432* (9).
Sandberg, J. H., D. T. MacDougal, & A. A. Heller. *130, 765* (9).
Sartwell, H. P., — (5).
Sarvis, J. T. *46* (9).
Scamman, E. *620* (3); *213, 1735, 3272* (4); *2402, 3369* (9).
Schallert, P. O. *5135* (4); *5136, 5963* (5); — (7a); — (9a).
Schedin, L. M., & N. T. Schedin. *602, 603* (9).
Scheuber, E. W. *28* (9).
Schmoll, H. M. *1050, 1268* (9a).
Schneck, J. — (5).
Schrader, F. C. — (4).
Schreiber, Beryl O. *2527* (2).
Schrenk, H. von. — (9).
Schrenk, J. — (4).
Schuette, J. H. — (4); *10* (9).
Schulz, E. D. *21* (8).
Scribner, F. L. *8c* (9).
Sellon, G. I. *85* (9).
Senn, H. A. *1334* (9).
Setchell, W. A. — (4).
Setchell, W. A., & H. E. Parks. — (9).
Seymour, F. C. *378*, S*378* (4).
Shafer, J. A. *58, 632* (5).
Shaw, C. H. *830* (4).
Shear, C. L. — (4); *47* (7); *4226, 4430, 4718, 4834, 5090* (9).
Sheldon, C. S. *340* (9).
Sheldon, E. P. — (4); — (9).
Shevkenek, W. *115* (9).
Shimek, B. — (7); — (8a).
Shinners, L. H. *3648* (5).
Shinners, L. H., & F. W. Stearns. *1696* (4).
Shockley, W. H. — (9).
Sholly, G. — (9).
Short, C. W. — (5).
Shreve, F. *5227* (9); *5426, 6285, 7332, 8012* (9a).
Shreve, F., & T. H. B. — (4).
Shriver, H. — (4); — (5).
Singer, J. W. *8* (5).
Skehan, J. — (7a); *87* (9a).
Small, J. K. —, *1291b* (4); — (5).
Small, J. K., & A. A. Heller. —, *9* (4).
Smart, Dr. *182* (9a).
Smith, A. D. *16* (9).
Smith, C., & F. Rindhart. *113* (9a).
Smith, C. C. *385, 505* (7); *505* (8a).
Smith, C. P. *3621* (2c); *1561, 2332* (9).
Smith, E. C. — (1).
Smith, G. — (7a).
Smith, J. D. — (5); — (7a).
Smith, P. — (2a); *11* (8a).
Snyder, Mrs. M. — (7).
Somes, M. P. *23* (9).
Sonne, C. F. —, *12* (2).
Soth, Mrs. M. E. *C-109* (9).
Sperry, O. E. *T171, T601* (8).
Spiegelberg, C. H. *202, 203* (9).
Sprague, R. *255* (9).
Spreadborogh, W. *70320* (9).
Standley, P. C. *6706* (2a); *5342, 12126, 16360, 18313* (4); *11291* (5); *4147, 5108, 6593, 15321, 17006* (9); —, *40615* (9a).
Standley, P. C., & H. O. Bollman. *10964* (9).
Stanfield, S. W. — (8).
Stearns, E. *348* (9).
Steele, E. S. *98* (5).
Steele, E. S., & Mrs. E. S. Steele. —, *149* (4).
Stephenson, B. C. — (5).
Stephenson, M. R. *171* (7a).
Stevens, G. W. *15* (7, 7a); *73.1* (7); *94.1* (7a); *192* (8a); *409, 507½* (9a).
Stevenson, E. *16* (9).
Stewart, L. M. — (4).
Steyermark, J. A. *237, 351, 420, 451, 553, 574, 4580, 4619, 4693, 4950, 8029, 10078, 10090, 10180, 10235, 10459, 18502, 18600, 18613, 18633, 18805, 18908, 19051, 21265* (5); *18636, 18757, 18760* (6); *554, 769, 4516, 4528, 4530, 4541, 4556, 4564, 4575, 4740, 5729, 8038, 18519, 18631, 18646, 18668, 18712, 18719, 18751, 18766, 18797, 18817, 18821, 18826, 18833, 18861, 18873, 19209, 19215* (7); *813, 10210, 10249, 10260* (7a).
Stillinger, C. R. *29* (2d).
Stillinger, R. C. *51* (9).
Stokes, S. G. — (9a).
Stone, Mrs. F. M. *266, 532* (9); *20, 78, 333, 444* (9a).
Storey, G. M. — (3).
Stratton, R. *676a* (7); *676b* (7a).
Studer, A. *4-16* (4).
Studhalter, R. A. *1173* (9a).
Studhalter, R. A., & J. Marr. *S-3015* (9).
Sturgis, W. C. — (9a).
Sturtevant, E. L. — (4).
Sudworth, G. B. *88* (4).
Suksdorf, W. N. *1948, 6666* (1); *3* (9).
Svenson, H. K. *4455* (5).
Sylvester, C. H. *30* (5).

Tarleton, J. B. *178a, 178b* (4); *49a, 49b* (9).
Tatnall, E. — (5).
Taubenhaus, J. J. *2787* (7a).

Taylor, B. *2301* (9).
Taylor, B. C. — (4).
Taylor, T. M. C., R. C. Hosie, R. E. Fitzpatrick, S. T. Losee, & A. Leslie. *1310, 1311* (4); *1314* (9).
Taylor, T. M. C., S. T. Losee, & M. W. Bannan. *505, 506, 508* (4); *502, 504* (9).
Taylor, K. A. — (5).
Texas, University of. — (7a); — (8); — (8a); — (9); — (9a).
Thames, L. — (9a).
Tharp, B. C. — (6); —, *35000, 37000* (7a); — (7b); —, *36000, 37001* (8).
Thompson, E. — (1).
Thompson, E. S. — (9).
Thompson, J. W. *630, 4110, 9409* (1); *13406* (2c); *7000, 8311, 11447, 11905, 13502, 14162* (9).
Thompson, J. W., & E. M. Thompson. *42, 209* (9).
Thompson, S. L. *30* (4); *97* (9).
Thornber, J. J. — (7); —, *5699* (9); —, *2822, 4053* (9a).
Thornber, J. J., & Brown. — (9a).
Thornber, J. J., & F. Shreve. *7809* (9).
Thornton, C. W. *319* (3).
Thousen, Mrs. O. T. *6* (3).
Thurber, G. *146* (9a).
Tidestrom, I. *3500, 3776* (2a); *333, 1879, 9468, 10935* (9).
Timmerman, M. — (4).
Tinsley, J. D. — (5).
Tolstead, W. L. *6898, 7074* (8).
Topping, D. L. — (4).
Tosh, J. P. *564* (4); *97* (5).
Toulouse, B. — (9a).
Toumey, J. W. *49* (9a).
Townsend, C. H. T., & C. M. Barber. *163* (9a).
Townsend, E. C. — (1).
Tracy, S. M. *9212* (7a); *37* (9a).
Tracy, S. M., & F. S. Earle. *392* (8).
Train, P. *2176, 2616, 3053* (9); *2536* (9a).
Trelease, W. — (4); —, *107* (5); — (9).
Trelease, W., & D. A. Saunders. *3872, 3873, 3874* (3).
True, F. W., & D. W. Prentiss Jr. *12* (3).
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EXPLANATION OF PLATE

PLATE 28

Generalized floral morphology of *Corydalis* drawn from *C. Caseana* Gray ssp. *Brandegei* (Wats.) Ownbey.

Fig. 1. Dorsal view of gynoecium.
Fig. 2. Lateral view of gynoecium.
Fig. 3. Unspurred stamen phalange.
Fig. 4. Exterior view of spurred petal.
Fig. 5. Interior view of spurred petal.
Fig. 6. Internal structure of flower showing arrangement of parts.
Fig. 7. Sepal.
Fig. 8. Exterior view of clawed inner petal.
Fig. 9. Interior view of clawed inner petal.
Fig. 10. Interior view of unspurred outer petal.

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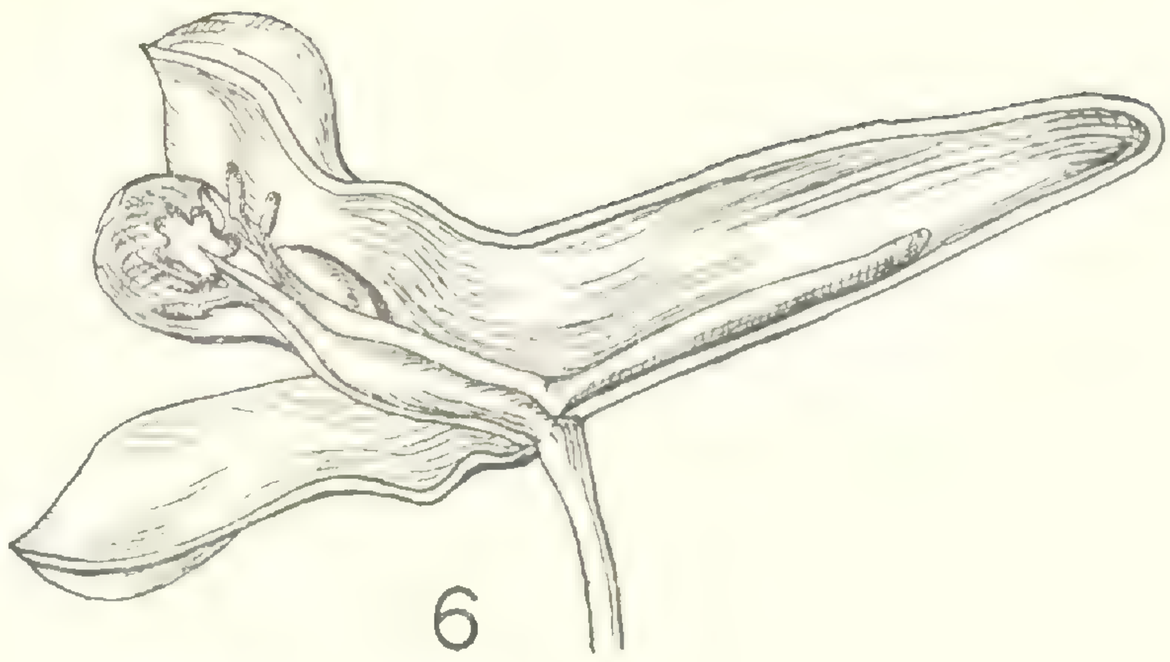

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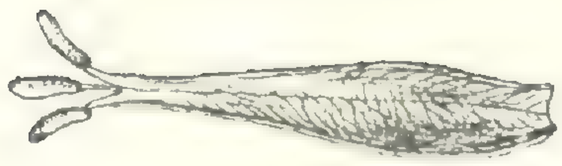

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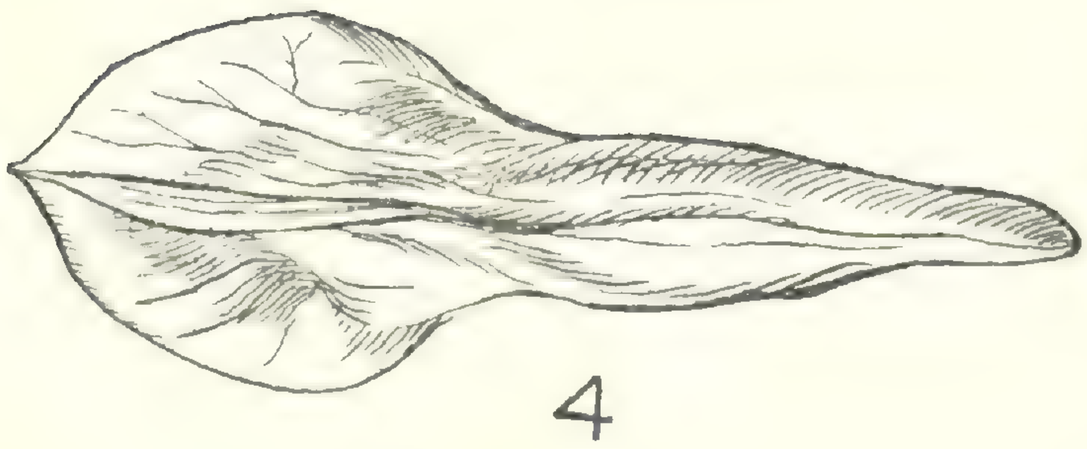

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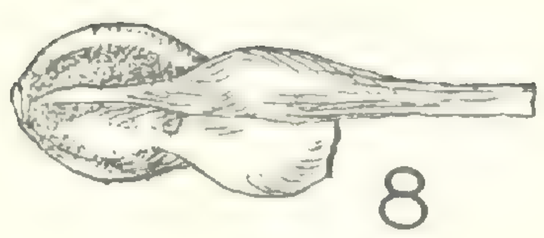

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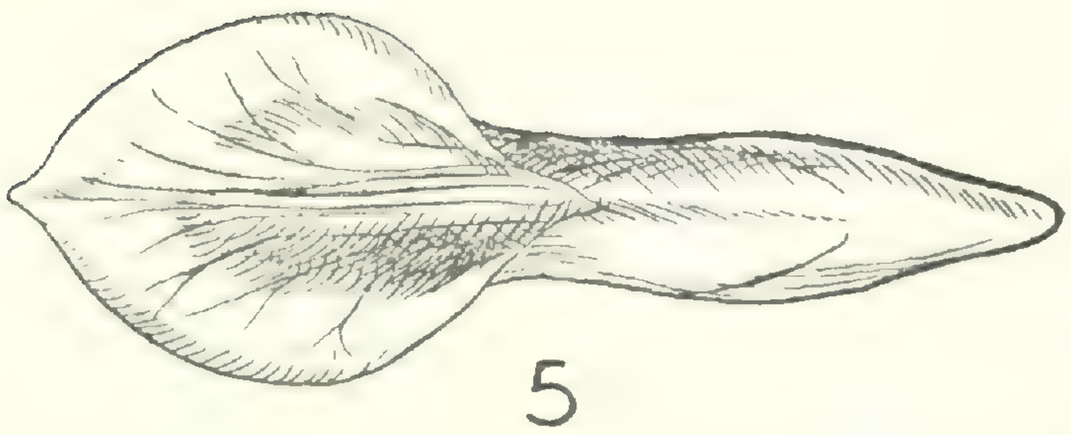

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Explanation of Plate

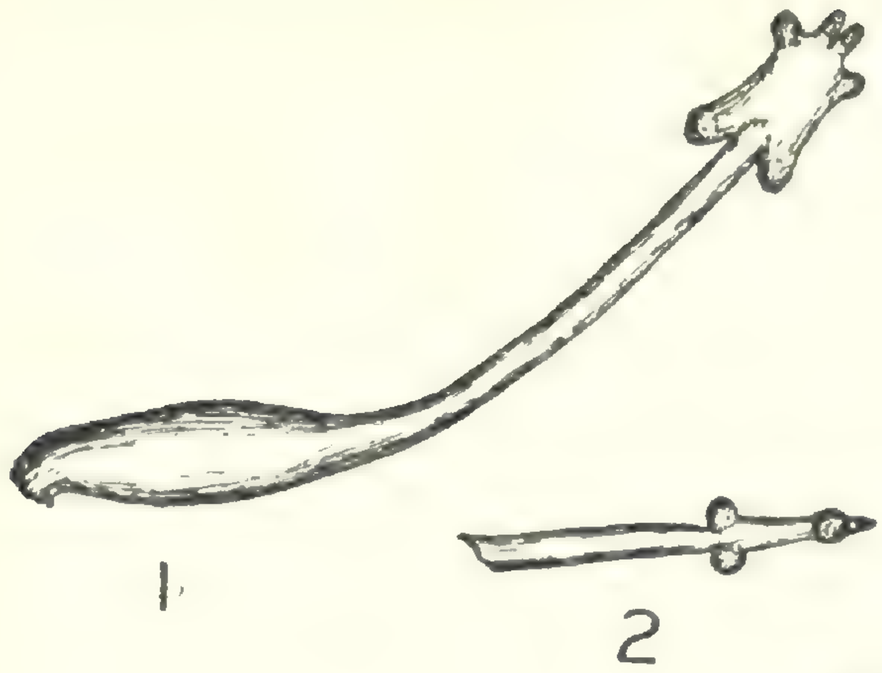
PLATE 29

Figs. 1–11. Gynoecia of species of *Corydalis* at flowering time; drawn especially to show morphology of the stigma. Each drawing is representative of all subspecies of the species; × about 8.

Fig. 1. *C. Caseana* Gray.
Fig. 2. *C. Caseana* Gray; side view of stigma.
Fig. 3. *C. Scouleri* Hook.
Fig. 4. *C. pauciflora* (Steph.) Pers.
Fig. 5. *C. micrantha* (Engelm.) Gray.
Fig. 6. *C. curvisiliqua* Engelm.
Fig. 7. *C. aurea* Willd.
Fig. 8. *C. flavula* (Raf.) DC.
Fig. 9. *C. crystallina* Engelm.
Fig. 10. *C. pseudomicrantha* Fedde.
Fig. 11. *C. sempervirens* (L.) Pers.

Figs. 12–15. *C. Caseana* Gray; drawings representative of Sections Ramoso-sibiricae and Pes-gallinaceus.

Fig. 12. Raceme in fruit; × about 1.
Fig. 13. Seed; × 4.
Fig. 14. Seed; × 2.
Fig. 15. Fruit, showing manner of dehiscence; × 4.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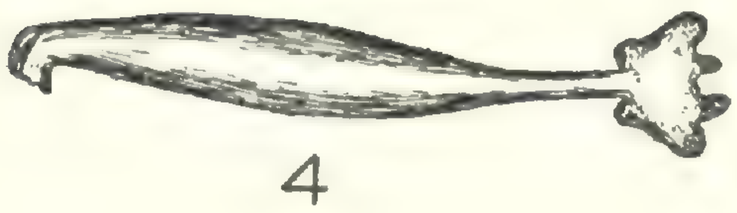
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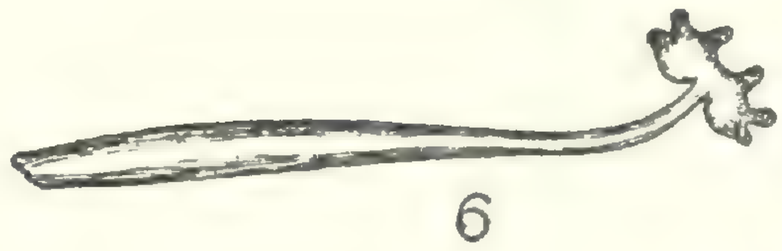
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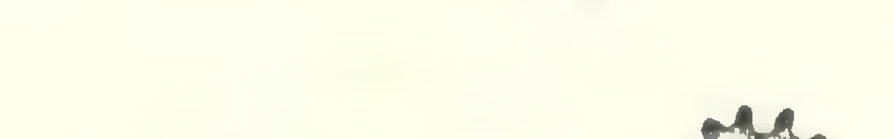
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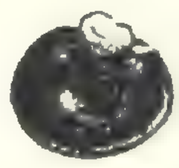
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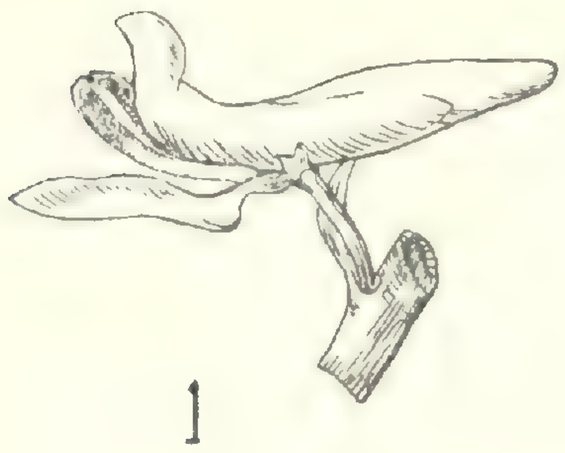
Explanation of Plate

PLATE 30

Flowers of the subspecies of *Corydalis Caseana* Gray and of *Corydalis Scouleri* Hook. An interior view of the unspurred outer petal is shown in each case to illustrate differences in structure; × 1½.

Figs. 1–3. *C. Caseana* Gray ssp. *Caseana* Ownbey.
Figs. 4–5. *C. Caseana* Gray ssp. *Brandegei* (Wats.) Ownbey.
Figs. 6–7. *C. Caseana* Gray ssp. *brachycarpa* (Rydb.) Ownbey.
Figs. 8–9. *C. Caseana* Gray ssp. *Cusickii* (Wats.) Ownbey.
Figs. 10–11. *C. Caseana* Gray ssp. *hastata* (Rydb.) Ownbey.
Figs. 12–13. *C. Scouleri* Hook.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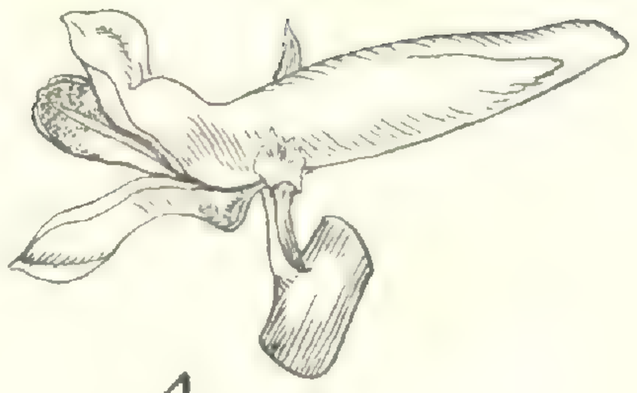
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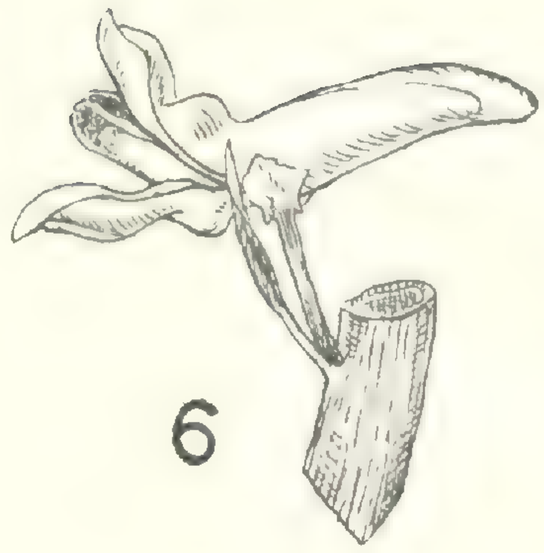
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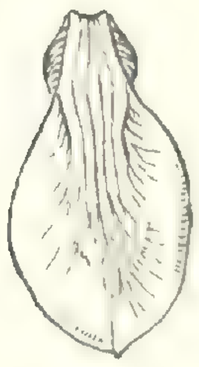
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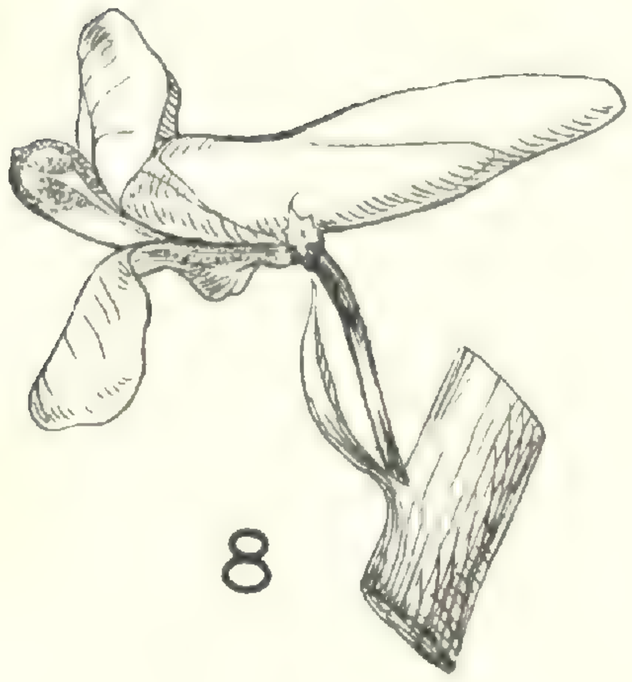
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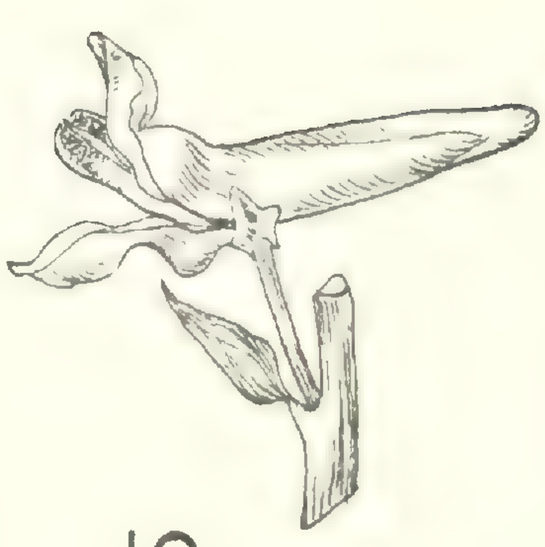
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Explanation of Plate

PLATE 31

Corydalis pauciflora (Steph.) Pers.

Fig. 1. Raceme in fruit; × about 1½.

Fig. 2. Habit of plant; × about 1½.

Fig. 3. Stigma; × 8.

OWNBEY—MONOGRAPH OF CORYDALIS

A STUDY OF HEVEA (WITH ITS ECONOMIC ASPECTS) IN THE REPUBLIC OF PERU[1]

R. J. SEIBERT[2]

Introduction

Natural rubber holds, and will continue to hold, a leading position among the commodities of the world. It is relatively a newcomer among the necessities of our advancing civilization, yet its absence would change the conveniences of modern life to drudgery.

Various articles made from *Hevea* were perhaps first described from the Amazon valley in 1535 by the historian Oviedo y Valdes. Two hundred years elapsed before La Condamine, during 1734-1744, brought out samples of rubber from the Amazon valley, introduced the strange material to European nobility, and later published his reports, which included a crude drawing of the *Hevea* tree. The *Hevea* rubbertree received its formal botanical treatment in 1775 by the French botanist Aublet, who described it as *Hevea guianensis* from material collected in French Guiana.

Colonial policies of rigid forign trade barriers prevented rubber from reaching the open market until after the Napoleonic invasion of Portugal. In 1823, however, the first commercial shipment of rubber reached the United States in the form of several hundred pairs of rubber shoes manufactured by the Para Indians. Stimulated by the invention of the vulcanization process by Charles Goodyear in 1839 and the great advances of the automobile industry of this century, rubber became the "gold" of the Amazon. An ever-increasing demand of a decreasing supply resulted in the decline of the Amazon jungle exploitation. Its complete collapse was brought about by the development of *Hevea* plantations in the British and Dutch East Indies, which, with their inevitable large-scale industry and consequent lower prices, rapidly took over world production during the second decade of this century. Since rubber was no longer supplied to the United States from South America, the penalty was paid during the recent war for virtual East Indian monopoly. We can appreciate, now, the efforts of our government in attempting to stimulate small farm rubber production throughout Latin America (Blandin, 1941; Klippert, 1942).

Since Aublet's first description of the genus *Hevea* in 1775, about 100 species, varieties, subspecies and forms have been described under various name combinations. Although *Hevea brasiliensis*, under cultivation, has been studied with con-

[1]An investigation carried out at the Missouri Botanical Garden in the Graduate Laboratory of the Henry Shaw School of Botany of Washington University and submitted as a thesis in partial fulfillment of the requirements for the degree of Doctor of Philosophy. Field observations and data were obtained in the course of the writer's official surveys and jungle exploration work during 1940 to 1946 as Botanist for the Division of Rubber Plant Investigations, Bureau of Plant Industry, Soils and Agricultural Engineering, Agricultural Research Administration, United States Department of Agriculture.

[2]Botanist, Division of Rubber Plant Investigations, Bureau of Plant Industry, Soils and Agricultural Engineering, Agricultural Research Administration, U. S. Department of Agriculture.

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siderable detail, little is actually known about it, and less about the other species as they occur naturally in the Amazon valley. The majority of collections and studies have been confined to the navigable rivers, a narrow margin away from these streams, and around centers of habitation. What *Hevea* forms exist, and how they exist, between the major streams and their headwaters in the eastern Andean foothill arc that skirts the range limit of the genus, will remain a question as long as interstream areas are undeveloped. This question will furthermore remain as long as transportation is largely confined to the main waterways and until more than an occasional individual with scientific interest studies the genus, its components, and its ecology.

Through the studies of Dr. Adolfo Ducke, the great authority on Amazonian botany, and those of Drs. Richard Evans Schultes and J. T. Baldwin, Jr., we are coming to realize that the specific entities of the genus are limited to less than a dozen. These entities can be rather clearly delimited morphologically and ecologically in spite of considerable intraspecific variation. It is becoming evident that both geographic and morphological forms are being established within the species, that interspecific hybridization frequently occurs in nature, and that apparently few genetic barriers exist between the species.

With the recent war-time stimulation to wild-rubber tapping in the Amazon valley, modern advances in transportation methods, and the ever-increasing need for plant improvement programs, the Division of Rubber Plant Investigations, U. S. Department of Agriculture, has pursued basic studies of *Hevea* in its natural habitats. In addition, it has undertaken the selection of superior strains of *Hevea brasiliensis*, as well as of other species and varieties from the jungles, and established them in Tropical American experiment stations where a planned system of *Hevea* plantation improvement is under way (Brandes, 1941, 1943; Rands, 1942).

Material and data derived since 1940 from the efforts of the Department of Agriculture, in cooperation with the Latin American Republics surrounding the Amazon valley, have augmented substantially our previous knowledge of *Hevea* as a whole. With such data we can begin to visualize in an over-all manner the morphology, taxonomy, distribution and genetics of the genus preliminary to a comprehensive monographic work, though many gaps remain to be filled in all countries concerned. Moreover, we can begin to make sound progress, through selection and breeding, toward the quality of planting material, disease resistance and adaptability, as well as increasing production while lowering costs.

SCOPE OF THE WORK

This study considers the genus *Hevea* as it is known to occur in the Republic of Peru. Although I devoted three years to its study there, and others before me have collected and written of the Peruvian species, vast areas exist between the relatively few stations studied for which hear-say and assumption still must take the place of accurate information.

It has, of course, been impossible to consider the Peruvian Heveas without first taking cognizance of speciation in the adjoining Amazonian countries, particularly in Brasil. The genus, besides being of great economic importance, has the distinction of being sharply confined within the *hylaea*, or Amazon River drainage basin, except in its northeastern distribution where the range extends to the watersheds of coastal drainage basins in the Guianas and to some extent in southern Venezuela.

Speciation in *Hevea* has been considered a difficult problem and has been treated in various fashions. Because the genus is composed mostly of large trees it not only has been difficult to collect but seldom has yielded complete study material. The result has been that species often have been described solely on sterile material, only to be described later as another species on the basis of fruiting or flowering material. Comprehensive studies of comparative morphology are lacking, although there has been some study of floral morphology, particularly by Hemsley (1898). Unfortunately, natural intraspecific variation has not been given due consideration; and an amazing number of prominent and reliable specific characters have been entirely overlooked.

Much of the following discussion will deal with several newly proposed floral and vegetative characters which appear to have constant specific value and are of great practical use to both the herbarium and the field worker. That such significant characters have been overlooked previously is further evidence that constant and repeated observation has no substitute for revealing new plant features. Characters present but not previously recognized for their value, or inspirations from that subconscious feeling of "indescribable differences," under repeated observation of the unit as a whole, may loom to the conscious as significant features in the key to solution.

This paper is of necessity provisional. It will try to bear out new evidence for speciation in *Hevea* along with that known and used in the past. An attempt is made to devise a practical key to the species which may be of equal use to the herbarium and field worker. For the first time it will bring together the taxonomy of the Peruvian Heveas as a unit, as well as those of the neighboring country, Bolivia. The paper will solicit trial by those who encounter this group of plants, and, it is hoped, will stimulate further comparative morphological observations by others, so that monographic treatment of the genus may be eventually in order. It will attempt to add its bit to the promotion of cooperation between the taxonomist and the geneticist, both of whom will have a long and fertile field of research in this highly important genus of trees.

Acknowledgments

To the Division of Rubber Plant Investigations, Bureau of Plant Industry, Soils and Agricultural Engineering, Agricultural Research Administration, U. S. Department of Agriculture, with which I have been associated as Cooperative Agent since July 1940, I am indebted for facilities and experience gained through their Plantation Hevea Improvement Program carried on in cooperation with

thirteen Latin American countries. The Division has kindly extended to me a year's leave of absence during which time it has been possible to continue my studies at the Missouri Botanical Garden.

Material for much of this paper was gathered from the Republic of Peru. I am deeply grateful for aid rendered by government officials concerned with the rubber program in that country. The Estación Experimental Agrícola de Tingo Maria, Peru, a cooperative agricultural experiment station maintained by the Office of Foreign Agricultural Relations, U. S. Department of Agriculture, and the Peruvian Ministry of Agriculture through its Peruvian and United States employees, was of constant aid in propagating and maintaining living material of jungle selections. To the many rubber tappers, *shiringeros* (Seibert, 1947), with whom I worked and lived, must go much credit. They are the men who help one in the "bush" when help is most needed. They are the men who know rubbertrees instinctively, and from them came many basic facts which we in return can put into scientific language.

Preparation of this paper has meant the amassing of most of the *Hevea* specimens from the major herbaria of the United States, namely, U. S. National Herbarium, New York Botanical Garden, Chicago Natural History Museum, Missouri Botanical Garden[1], Gray Herbarium, Arnold Arboretum, and the National Arboretum, to the curators of which I am indebted for loaned material.

Dr. John T. Baldwin, Jr., and Dr. Richard Evans Schultes, both of whom are actively concerned with somewhat similar studies in other Amazonian countries, have made available to me their collections of *Hevea*. They have been most considerate and helpful in discussions, both verbally and through correspondence, and have tested for me a number of morphological characters here proposed. Mr. Hans Sorensen, Agent, Rubber Plant Investigations, stationed at the Instituto Agronomico del Norte, Belem, Brasil, has kindly tested and confirmed my observations regarding the question of short-shoots. Dr. John B. Carpenter, Agent, Rubber Plant Investigations, stationed at the Estación Experimental Agricola de Tingo Maria, Peru, very kindly has forwarded to me herbarium speceimens of critical material from my living jungle selections as they have come into flower since my departure from Peru. To these institutions and individuals and to many others who have been of aid in this phase of the Hevea Improvement program, I wish to express my appreciation for the fine spirit of whole-hearted cooperation which is so much needed in coordinating large-scale programs of national and international extent.

Morphology of the Genus

Habit.—

Without exception the genus is woody. For the most part it is composed of medium-sized to large trees, which in *Hevea guianensis* var. *lutea* and especially *H. brasiliensis*, frequently may reach 45 meters in height under most favorable growing conditions. Largest trunk diameters are found within *H. brasiliensis*, and in Madre de Dios, Peru, it is not uncommon to find trees 1 meter, occasionally 1.5

[1]To Dr. Robert E. Woodson, Jr., I am indebted for valuable guidance of the research and presentation of the morphologic and taxonomic aspects of this paper.

meters, in diameter at 1 meter above the ground.

In contrast to the large trees of the genus, two entities have been reported in which the habit is low and shrubby. The case of *H. camporum* Ducke (1925), collected by R. Monteiro da Costa in the *campinas*[2] between the headwaters of the rivers Manicore and Marmellos, southern tributaries of the lower Madeira, is very poorly understood because of sparse herbarium material collected. The region from which it comes apparently is hilly, semi-open, grassy and scrub-forest land, unfavorable to good tree growth. According to Ducke (Schultes, 1945) the species perhaps is only a dwarf form of *H. pauciflora* var. *coriacea.*

The other interesting case of dwarfed or shrubby habit in the genus is *Hevea nitida* var. *toxicodendroides* (Schultes, 1947), discussed by Schultes (1944) and described as *H. viridis* var. *toxicodendroides* Schultes & Vinton. This variety was discovered in Colombia from the upper Apapores Basin, growing on and around apparently old sandstone outcrops of at least Triassic age, on which semi-xerophytic conditions exist. These plants are about 12 feet tall and are quite bushy or shrubby in aspect. Otherwise they resemble the species in morphology and size of the leaves, flowers, fruit and seed. Thus it appears that variation may be more ecological than morphological. Experimental growing only can determine this.

From apparent intergradations between the normal type of tree branching and the low branching of the shrubby types one may observe and interpret conditions frequently encountered in plantations of the commercially grown *H. brasiliensis.* Pruning is a common practice and certain "clones"[3] under normal conditions tend to form a low branching habit. It is necessary, through pruning, to prevent the formation of such low branches as it would interfere with a good tapping panel. Under conditions of undue drought and where soil is not suitable for growth of *H. brasiliensis* almost all individuals of the species will tend to have profuse and low-branching habits, not at all typical of the same plants growing under natural conditions.

Trunk.—

Growing under flooded conditions, where the trees stand in various depths of water for nearly the entire year as do *H. Spruceana, Benthamiana* and *microphylla*[4], the trunks are distinctly swollen toward the base. This "bellying" is pointedly referred to by the Brasilian name for *H. Spruceana, seringueira barriguda*[5]. The amount of bellying and the height to which it extends may possibly be some indication as to how high flood waters reach up the trunk. Above the uniformly swollen portion, the trunk suddenly tapers upward. A graphic example of this bellying effect due to flooding appears to be well illustrated by contrasting the *H. brasiliensis* of the periodically inundated land, *tierra baja*[6] of the upper Amazon proper,

[2] *Campinas* in Brasil refer to grassy, scrub-forest hilltop land.

[3] A clone in *Hevea* plantation terminology refers to an individual tree which is vegetatively propagated through successive generations by means of bud-grafting.

[4] Schultes ('47) has shown from type studies at Kew that *H. minor,* as at present known, should be referred to *H. microphylla.*

[5] *Seringueira barriguda* in Portuguese means big-bellied rubbertree.

[6] *Tierra baja* in Peru refers to low inundated land along rivers; and *tierra altura* to land above the level of river flooding.

with that growing on well-drained *tierra altura* of Pando in Bolivia and Madre de Dios in Peru. Wherever the trees are subjected to periodic inundation the swollen bases are conspicuous and rather suddenly tapering several feet above the ground. On *tierra altura* the trunks are definitely cylindrical with no more than the normal gradual tapering in girth.

The normal trunk for the species growing on well-drained land is cylindrical to the ground level with a very slight tapering or girth decrease upward. Under usual forest conditions the first branches depart from the upper third of the tree. It is not uncommon to find forest giants with 90 to 100 feet of cylindrical trunk to the first branches.

There appears to be no reference to, nor have I seen any cases of buttressing. However, Dr. Baldwin informs me that he found a buttressed tree on the Rio Negro, which he is inclined to feel resulted through intergeneric hybridization with *Cunuria*. It would appear that buttressing is not a characteristic of *Hevea*.

Interesting evidence concerning the age of *H. brasiliensis* trees from Bolivia and the Acre Territory of Brasil is given by La Rue (1926). These areas and that of adjoining Madre de Dios, Peru, are characterized by having one distinct rainy and one distinct dry season per year, conducive to the formation of annual tree rings. Although no increment borer was available, I was able to observe the trunks of a number of trees at Iberia, Peru, which were felled to make way for an air strip. Annual rings were not noticeable until nearly a year after felling, when partial decomposition of the wood had set in. A radial cross-section of one of these trees, 84 cm. in diameter, showed 211 annual rings. There is indeed little doubt that some of the largest forest giants were already growing before the discovery of America.

Bark.—True outer bark color and other characteristics in *Hevea* are often distinctively overshadowed by the predominance of crustaceous lichens which makes the trees easily spotted in the forest. As yet there has been insufficient investigation and description of the bark as applied to specific delimitation. In general, it is quite smooth with some scaling and color range from light gray to dark brown. There appears to be much intraspecific variation in bark characters, ranging through very smooth, pustuled, flaky, shaggy, to definitely corky within *H. brasiliensis* itself. An extreme has been described by Bartlett (1927) as *H. brasiliensis* mut. *Granthami*. Bark variants of this and many other types occur not only in plantation material but in the wild as well, together with the intergrading forms. Schultes (1945) reports evidence from Colombia that bark variations are of importance in distinguishing subspecific variants in *Hevea*. These bark variants are important factors in a selection of trees for plantation use, in that ease of tapping may be considerably hampered by such rough strains. Outer bark variations would appear to be of considerable use in clone distinction (Frey-Wyssling, 1933).

The inner portion of the bark, or phloem, is, from the economic standpoint, the important part of the tree anatomy, since the latex vessels located here furnish the natural rubber of commerce when cut in the process known as "tapping."

Here again there may be as much or seemingly more intraspecific as interspecific variation. Within *H. brasiliensis* the phloem of mature trees may vary in thickness from about 0.5 cm. to about 2 cm. Apparently, due to the cambial development of concentric rings of phloem, the latex vessels occur in concentric rows, the number of which is highly variable, ranging from about 8 to 35. There would seem to be no correlation between number of latex rows, their individual size or productivity, and age or size of the mature tree. Perhaps one of the most striking variations in phloem is the color. This variation, or series of variations, for *H. brasiliensis* appears to reach its maximum toward the southwestern and western part of the species range. Observations of thousands of trees seemingly have shown all range of variation through tan, brick, purplish red, reddish purple and blackish purple. La Rue (1926) has a considerable discussion of these color variations. There is a feeling among the rubber tappers that the trees with purplish phloem, and particularly those with the *preta*[7] or blackish purple color, give the best yield and the superior quality of rubber. Although there may be such a tendency, this color is by no means a constant criterion as evidenced from jungle selection work carried on in the Madre de Dios area.

Texture of the phloem likewise is variable, ranging from very hard, with high number of stone cells, and difficult tapping, to soft, easy-cutting, almost "cheesey" texture. There seemingly is a tendency for trees with purplish phloem to have a softer texture than those with more tannish phloem. It is interesting to note that though a tree may have virgin bark of a tannish or light-colored phloem, the renewed phloem from previously tapped portions of the same tree has a reddish or purplish color. Trees with a reddish or purplish virgin phloem, as well as those with renewed secondary reddish or purplish phloem which is tan in virgin condition, often exude a reddish or purplish dye-like fluid independent of the latex flow when freshly cut.

With the exception of the seemingly complete absence of so-called *preta* trees from the lower Amazon region, there would seem to be no geographic, ecologic or edaphic range limitations of these various bark variations. Any randomly selected *estrada*[8] from the Madre de Dios may contain a fairly complete range of color and other bark variations within close proximity. There furthermore is no conclusive evidence from the Madre de Dios region that any of the numerous bark variations are constantly associated with such intraspecific morphological variations as leaf size and shape.

Although little is known of bark variations in other species than *H. brasiliensis*, it appears that similar variations exist in *H. guianensis* var. *lutea*. Here the outer bark also shows variations in type and amount of scaling. The phloem color ap-

[7] *Preta*, meaning black in Portuguese, is used to describe trees of *H. brasiliensis* in which the phloem is distinctly blackish purple in color.

[8] An *estrada* consists of about 100 to 150 rubber trees, joined one to another by a forest trail running from and returning to the *shiringero*'s house in somewhat loop fashion. A map of an estrada has been excellently figured by Preusse-Sperber (1916). The rubber tapper is usually assigned two estradas, the trees of each being tapped on alternate days.

pears to vary from light tan to a somewhat purplish red. The texture and thickness also are quite variable.

Latex.—Slight chemical differences distinguish the rubber from the latex of the different species. Great differences, however, do occur when the latex as a whole, including its serum and non-rubber content, is taken into consideration (Parkin, 1900). It is well known that *H. brasiliensis* as a species gives the most abundant yield and the best quality of rubber from the manufacturing standpoint, while *H. Benthamiana* probably ranks second. It is also true, but less well known, that in the species *H. brasiliensis*, within areas of its distribution as well as between its regions of distribution, there are great variations in these qualities. On the basis of these facts, large-scale selection and later breeding programs in the Far East have been able to step up yields per acre from less than 450 pounds annually to recent experimental yields as high as 2000 pounds. Such has been done from the original stock of less than 100 trees of *H. brasiliensis*[9] finally surviving from those introduced by Henry Wickham into Ceylon and Singapore from seed he collected near Boim, Rio Tapajoz, Brasil. From this might be visualized ultimate yield possibilities by choosing stock from such areas in the southwesternmost limits of *H. brasiliensis*, as in the Madre de Dios, where average tree yields are proving to be some three times as great as the region from which the Far Eastern stock was obtained.

Although *H. guianensis* and its varieties may be characterized partially as having yellow latex and considered as having low yields of weak rubber, there is a great deal of tree to tree and area to area variation. It is usually noted within this group that the color of the latex may become nearly white after successive tapping over periods of time. Latex color appears to be no criterion of quality inasmuch as both *H. brasiliensis* and *H. Spruceana* are characterized by white latex. The former species produces excellent quality and the latter very inferior quality shunned by all rubber tappers. Cases of latex reaching sulphur-yellow tones are known to exist in *H. brasiliensis*, both among plantation-developed clones and among jungle trees. There is no evidence that such individuals produce inferior rubbers. Trees have frequently been found in the jungle selection work where the latex of the young branches is yellow, while that from the trunk is perfectly white.

Cases are known where the latex is very high in resin content, producing a very "tacky"[10] rubber. Such occurrences are frequent in areas below Iquitos where apparently introgression of *H. pauciflora* into the *H. guianensis* complex has resulted in the weakening of the rubber to such an extent that freshly coagulated rubber fails to keep its shape even over night. *H. pauciflora* itself has a very poor resiny rubber and never is tapped commercially. Allen *(No. 3298)* reports a

[9]According to Mann (1940), "It seemed fairly clear, however, that the whole of the rubber in Malaya originally came from 27 seedlings of the original Wickham collection that went to Singapore in 1876."

[10]"Tacky" rubber is that which in coagulated form remains resiny and sticky, refusing to maintain its original shape. It is usually very weak with little elasticity.

collection of *H. nitida* from the Vaupes region of Colombia, in which adulteration of the latex with that of good latex from other species resulted in the ruining of all the latex, even preventing proper coagulation.

Latex yield, and often its color and quality, cannot be gauged from the first incision made into the tree. Both plantation and jungle tappers have found that the normal tree is stimulated by what is termed "wound response"[11] under systematic tapping. Yields from the individual tree increase as much as 20 per cent after several tappings or even several weeks of tapping, and so long as regular systematic tapping is carried on this optimum yield is obtained. On the other hand, rare cases have been seen in which the tree gradually "drys"[12] by the same system.

Latex flow from tapped trees is, of course, affected to some extent by the water content of the latex. Individual trees in the same jungle area will show considerable normal deviation from the accepted average of about 30–33 per cent Dry Rubber Content (DRC) and appear to range from between 20 per cent to as high as 45 per cent DRC. Seasonal variations also occur and lag somewhat in direct proportion to the amount of rainfall. A climate with a more or less uniform rainfall throughout the year and with no long pronounced dry season would be necessary if year-around tapping were desired. A further factor affecting latex flow, and one which is poorly understood, seems to be related to temperature and time of day at which tapping is done. Plantation experiments appear to have proved that flow and yield are substantially larger if tapping is done very early in the morning, before the sun reaches its full effect, or before 10:00 a. m. Furthermore, on cloudy days the time of maximum flow is extended considerably. Similar effects have been observed by the jungle tappers and apparently is in part directly responsible for the custom of many tappers to rise as early as an hour or two before sun-up and start their work with the aid of a lantern. During abnormal periods of cold weather in the upper Amazon regions[13] it also has been observed that tree yields considerably increase above normal.

Branch system.—

The normal branch system of the genus is composed of the prominent erect main axis from which arises a symmetrical system of secondary branches. Under usual forest conditions branching is found on the upper one-half to one-third of

[11] "Wound response" (Royal Botanic Garden, Ceylon, 1899) is the plantation term given to the normal increase in a tree's yield induced by systematic regular tapping over a period of days or weeks, from the comparatively low first-tapping yield to the normal yield of the same tree after it is in regular tapping.

[12] It is frequently convenient, when speaking of *Hevea* trees, to use the terminology of the dairy industry. To go "dry" is one of those terms.

[13] A rather broad area of the upper Amazon valley, roughly between Porto Velho and the Andean foothills, is subject to yearly cold periods lasting about 2–3 days known in Brasil as *friagem* and in Peru variously as *friaje* or *taraza*. One or more of these periods usually occurs around the months of July or August during which time strong southeast winds, recorded at Maldonado as high as 100 mph., precede a driving rain of short duration. This is followed by lighter winds, cloudy weather and temperatures as low as 10° C.

the tree. Radical exceptions to this form occur in *H. camporum* and *H. nitida* var. *toxicodendroides* which are characterized by low shrubby forms. Wind damage to forest trees, as well as artificial topping or pollarding occasionally practiced in plantations, appears to have similar effects in stimulating strong lateral branch development. There also would seem to be inherent branch differences among individuals or strains of the same species.

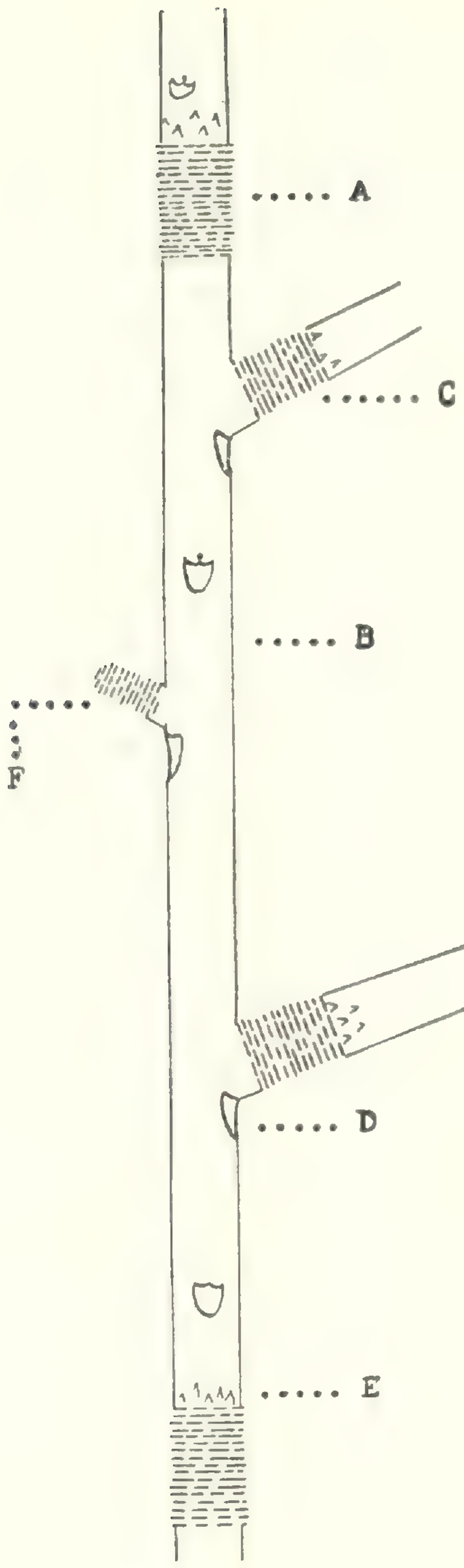
Two major habital forms within *H. brasiliensis* may be observed: (1) possibly the typical form in which there is a prominent main axis with small lateral branches; and (2) the form with lateral branches as prominent as the central axis and frequently even replacing it. Although plantation material appears to be largely of the latter type, representatives of the former also occur. Seed progeny from the low-river areas, as Belem and Rio Tapajos, as well as from such up-river areas as Acre, Madre de Dios and Iquitos, all growing at the Estación Experimental Agrícola de Tingo Maria, show both types of branching and intermediates to exist from all areas. There is a tendency, however, for the latter type to predominate in progeny from low-river areas, while the former appears to be predominant in up-river areas.

Another branch variation, discussed with reference to clonal differentiation by Frey-Wyssling (1933), concerns the angle and form at which the lateral branches arise from the main axis, being from nearly vertical to nearly horizontal. Until we have more information from both natural and cultivated habitats for all of the species, branching habits would seem to be primarily intraspecific variations and of more use in clonal than in specific delimitation.

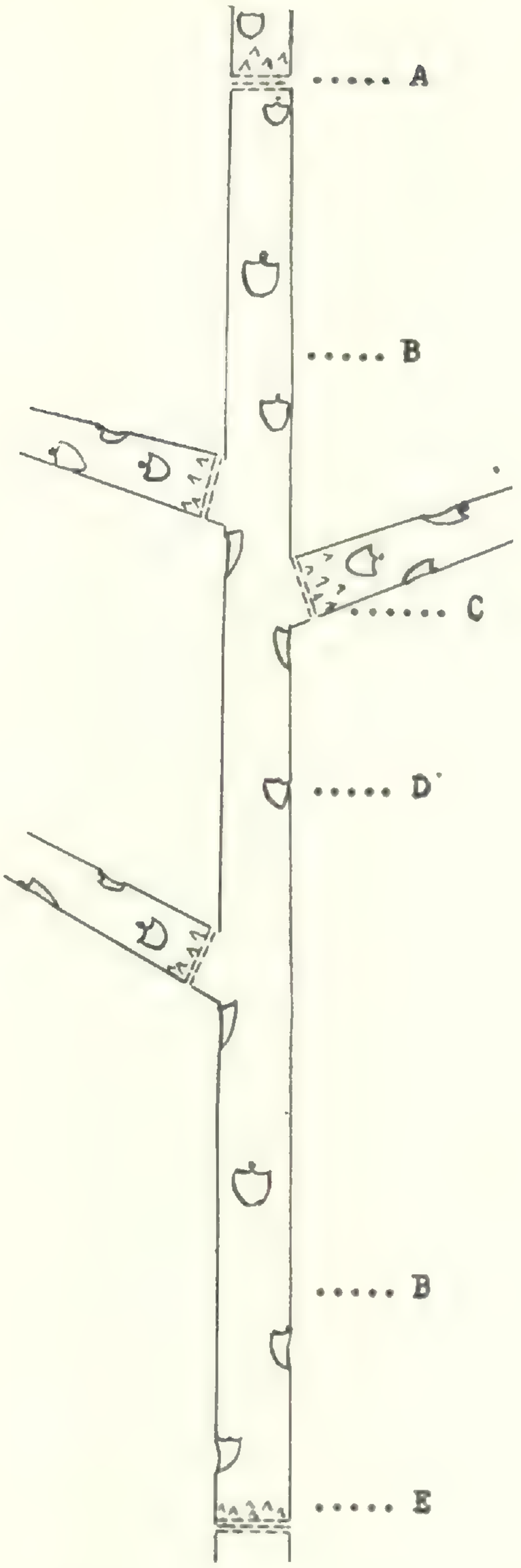
Roots.—

With the exception of *H. brasiliensis*, and to some extent *H. guianensis* with its variety *lutea* and *H. Spruceana*, little is known of the *Hevea* root system. A long, prominent tap root seems to be the rule, and also that rather prominent laterals radiate out from just below the ground surface to form a surface-feeding network. Under certain cultivated conditions, such as are found at Bayeux, Haiti, where a permanent high water table lies one and a half to three feet from the surface, the long tap root of *H. brasiliensis* either branches profusely at the water table or suddenly turns and follows parallel with it. In the Madre de Dios region where the species grow naturally on well-drained land, the root system is as found under normal plantation conditions. In the Iquitos area, where the species naturally grow part of the year in several feet of water and the rest of the year with a comparatively low-water table, the roots of several trees, uprooted by high winds, also have been found to be of the normal type. I know of no reference to the root systems of such species as *H. Benthamiana, microphylla* and *Spruceana*, which naturally grow permanently in water. *H. Spruceana*, however, does react normally in its root development when planted on well-drained land.

Long-shoots and short-shoots (Flushes and Interflushes): The genus *Hevea* is characterized by periodic (annual except in seedling stage), rapid stem growth or elongation alternating with a long period during which stem elongation



Text-fig. 1. Leafy shoots (flushes) alternating with relatively elongate caducous-scaly short-shoots (interflush short-shoots): A—conspicuous interflush short-shoot; B—long-shoot or flush; C—lateral branch development from a short-shoot or spur; D—leaf-scar; E—leaf scales on lower part of flush adjoining the short-shoot; F—lateral spur development.



Text-fig. 2. Leafy shoots (flushes) alternating with narrow rings of bud-scale scars (interflush rings): A—inconspicuous interflush short-shoot; B—long-shoot or flush; C—lateral branch development from an inconspicuous short-shoot; D—leaf scar; E—leaf scales on lower part of flush adjoining the interflush ring; lateral spur development inconspicuous.

and leaf formation are arrested or reduced. These intervals of rapid stem development or long-shoots have been referred to in plantation use as "stories" (Frey-Wyssling, Heusser & Ostendorf, 1932) and perhaps more popularly as "flushes" (Assoc. Cent. Exp. Sta., 1939). With the exception of noting the presence of terminal bud scars, and of scale buds at the area between "flushes," the center of the "corona"[14] region in budding terminology, little attention has been paid to this character in specific determination. It appears that the interval between flushes, or terminal bud scar region (text-fig. 1), might best be known as the "interflush" which, perhaps, is referable morphologically to a "short-shoot" (pl. 32, fig. 2).

No literature has yet come to my attention making any reference to one of the most striking morphological characters in the genus *Hevea*—the "short-shoot." The short-shoot, or spur, is well known in *Ginkgo* (Collins, 1903) and a number of conifers (Chamberlain, 1935). Short-shoots occur in the rosaceous fruit trees. They would appear to occur on the underground rhizomes of *Poa* and perhaps other grasses including Bamboo (note figs. 23 & 123 in Arber, 1934) and may be found in some of the higher plants, both tropical and temperate. It would not be hard to presume that a comprehensive study of short-shoots throughout the plant kingdom not only would furnish an interesting field of research, but also might lead to important taxonomic and evolutionary data.

Short-shoots generally have been given attention only when they develop prominent lateral spurs. They may continue for several years before suddenly changing their growth nature by transformation into a long-shoot. However, close examination shows that they may, and frequently do, occur terminally on the main axis and later are seen to be alternating between two long-shoots. Due to much compression of the internodes on these shoots, the normal long-shoot leaf phyllotaxy superficially appears to be changed. Furthermore, the leaves arising from these short-shoots are not entirely normal (Chamberlain, 1935).

In collecting *Hevea* for the herbarium, branching specimens are seldom chosen for the press. Thus little evidence of the presence of spurs is ever presented to the herbarium worker. In *Hevea* the short-shoots are not prone to linger for several years before developing into a long-shoot, though such has been seen on rare occasions. Ducke (1935) apparently came close to recognizing their presence, when, in his description of *H. guianensis*, he remarked: "Old branchlets with persistent scales at the terminal bud," and with regard to *H. Spruceana* pointed out "the numerous pointed scales which cover the vegetative buds."

Since, in the plantation, only *H. brasiliensis* has been under critical observation, and since short-shoots are so condensed (text-fig. 2) in this species as to be represented by little more than a narrow ring of a few scale bud scars between flushes (pl. 32, fig. 1), the character for the genus as a whole has not come into recognition. Even the classic work of Parkin (1904) on nectiferous and non-nectiferous

[14] "Corona" is a term being adopted by the U. S. Department of Agriculture to the area of the stem on which the buds are most crowded together.

bud scales fails to recognize the presence of the short-shoot. Furthermore, in the nursery where close observation might well bring out such a feature, we find that young *Hevea* seedlings and buddings have somewhat different vegetative habits from older trees. The young plant sends out a new vegetative flush barely after the previous one has matured. All the leaves from several flushes are persistent, whereas after the tree reaches about three years of age it will normally send out only one flush per year and that only after defoliation of the previous one, as in the case of *H. brasiliensis*. It is only after growth-habit maturity has been attained that the species showing distinct short-shoots will develop the character. We have a rather parallel condition in *Ginkgo* where the young plant develops only long-shoots until after it has reached some size.

The length of the flushes appears to be quite variable from year to year, probably depending both upon climatic conditions and upon the amount of shading the branch has received from other branches. From this standpoint the short-shoots of any one species appear to be less variable in length by comparison. As yet no instance has been seen where the short-shoot grades imperceptibly into the long-shoot.

The short-shoot in *Hevea* makes its terminal (and axillary) appearance during the maturation period of the flush and reaches conspicuous proportions just before the appearance of the inflorescence (pl. 33, fig. 1). In the species where the short-shoot is pronounced (*H. guianensis, Spruceana, pauciflora, rigidifolia* and *nitida*) it consists of a segment about 1 cm. long (pl. 32, fig. 2; pl. 33, figs. 2-3) covered with caducous scales (pl. 33, fig. 1-2) which morphologically are reduced leaves (Frey-Wyssling, Heusser and Ostendorf, 1932). The nodes of this portion of the stem are much compacted and number as many as 100, with internodes naturally being obsolete. The first branches of the inflorescence seem to arise from the axils of the uppermost scales (pl. 33, fig. 2) and shortly may be followed by the appearance of the young long-shoot or flush carrying the leaves. Frequently inflorescence branches also arise from the axils of the lowermost leaves of the long-shoot. On the older portions of the stem these short-shoots alternate with the long-shoots and are conspicuous at the interflush regions (pl. 33, fig. 3).

In those species where the short-shoot is much condensed or inconspicuous (*H. brasiliensis, microphylla* and *Benthamiana*—pl. 32, fig. 1), one not familiar with the genus as a whole might have difficulty in recognizing it as such. Nevertheless, the short-shoot is morphologically the same as in the previous group except that the scales or reduced leaves are very few and can be recognized at the interflush areas of the older stems as only a narrow ring of few bud-scale scars.

Cases of both natural and artificial hybridization between species of contrasting short-shoot condition, as *H. brasiliensis* × *Spruceana, H. Benthamiana* × *guianensis, H. brasiliensis* × *pauciflora*, etc., appear to show the conspicuous short-shoot, indicating its probable dominance as a factor in contrast to its opposite extreme in which the short-shoot is represented by an inconspicuous narrow ring of bud-scale

scars. Hybrids frequently appear which closely resemble the species except for having the conspicuous short-shoot. Such cases must be borne in mind when occasional specimens of *H. Benthamiana* varieties, for example, refuse proper placement in the proposed taxonomic key.

This conspicuously contrasting character is considered here as being of key significance in dividing the genus as a whole into two groups. Whether or not these two groups are entirely natural has not yet been determined; in fact, in combined consideration with many floral characters they do not appear to be entirely natural. Nevertheless, these divisions seem to be of more practical importance than previous ones based on anther number and anther whorls. It is hoped that further detailed study may be given to the question of short-shoots by others engaged in *Hevea* field work.

Leaves.—

The general structure of the leaf is uniform throughout the genus, being digitately 3-foliolate with the leaflets joined to the relatively long petiole by noticeable petiolules. A small, lateral, early caducous stipule is found on the stem at each side of the petiole base. Although 3 leaflets are the rule, 1, 2, 4 or 5 leaflets, or two of the leaflets grown together in varying degrees, may be found on rare occasions (Frey-Wyssling, 1931). Such abnormalities are found in both the plantation and jungle where either an occasional leaf may be abnormal or many of the leaves from the same tree show such conditions. Seedling leaves, so far as I have been able to observe, likewise normally are 3-foliolate. When leaf abnormalities do occur there seems to be a stronger tendency for the production of more than 3, rather than fewer leaflets. Conspicuous glands, or extra floral nectaries, which normally occur on the upper surface of the petiole just below the junction of the 3 petiolules, are apt to be extremely variable even on the same tree. It is from these petiolar glands that extra leaflets appear to be derived, and they may or may not be of stipular origin.

Phyllotaxy has been determined for *H. brasiliensis* (Ostendorf and Ramaer, 1931). Leaves are spirally disposed on the flushes and diverge at an angle usually of 138° (2/5) or occasionally at 103° (2/7). This appears to be the extent of variability throughout the genus. Some deviation from this might be expected in the bud scales or on the short-shoots of other species. A comparative study from fresh material will be undertaken at a later date in connection with a thorough consideration of the short-shoot within the genus.

Frey-Wyssling, Heusser, and Ostendorf (1932) have discussed in detail the tremendous variations of all parts of the leaf in *H. brasiliensis*. Observations on both field and herbarium specimens of other species indicate considerable intraspecific leaf variation to be characteristic throughout the genus. With some striking exceptions, which will be pointed out in the following paragraphs, leaves hold greater significance and consistency in distinguishing individuals or clones than for specific distinction.

Leaf persistence: Those who have observed *Hevea* growing, both in the plantation and in the Amazon valley, are familiar with the deciduous wintering habit of *H. brasiliensis*. During or near the end of the dry season it "winters" by losing all the leaves of the most recent flush and going through a dormant period of several weeks. The dormant period is followed by the appearance of inflorescences and, immediately after, the rapid growth of the new vegetative flush (pl. 34, fig. 1).

Under jungle conditions in any limited region, the trees of *H. brasiliensis* usually go through these stages at the same time, any one tree not lagging or being advanced by more than a few days. Under plantation conditions, particularly where there is no pronounced dry season or in abnormal latitudes or altitudes, the leaf-shed and flowering seasons may vary several months from tree to tree. In some extreme cases the same tree may be in several stages at the same time. Some branches may be defoliating and resting, others sending out inflorescences and young flushes, while still others may have mature vegetative flushes and already maturing fruit. Yet, so far as I am aware, within *H. brasiliensis*, the previous flush always defoliates completely before the appearance of the inflorescence on that particular branch. It is said that a few oriental clones[15] tend to hold their leaves while flowering, but the details are not clear to me. I am of the opinion that the actual branch which is flowering has defoliated; or, it may be that the clone is not genetically pure for the species. Such instances have been observed at Tingo Maria and Iquitos where individuals of Iquitos origin (referable to *H. brasiliensis* but very likely carrying genes of another species) hold a few leaves on the previous flush while flowering.

It should be explained that plants up to about three years of age do not show this seasonal wintering. They normally send out new flushes regularly every month to six weeks. During this stage of growth, leaves of about the top three flushes persist while those on the lower ones gradually absciss. The transition from this habit to the mature growth habit is sharp. At the proper age and size the young plant undergoes complete defoliation and continues thereafter to send out yearly flushes which completely defoliate before the appearance of the next flush.

There is good reason to believe that the *H. brasiliensis* type of defoliation and wintering does not occur in all species of the genus. No information on the subject appears to be recorded, and detailed field study of the flush and inflorescence habits of the genus as a whole is wanting.

The contrasting condition seems to exist in which leaves of mature tree flushes are persistent until well after the appearance of the inflorescence, its maturation and the presence of the new flush (pl. 33, figs. 2-3; pl. 34, fig. 2). It is not clear what, if any relationship exists between interflush rings and interflush short-shoots and the degree of dormancy. Unfortunately, insufficient field evidence is available

[15]Oriental clones are those developed and selected from cultivated *Hevea brasiliensis* growing on Far Eastern plantations.

to draw final conclusions, particularly from cultivated conditions where all the species are growing together in the same climate and soil. Mostly from evidence of herbarium specimens, the following categories appear to be evident with reference to the various species:

1. Leaves persistent on the previous year's flush until well after the appearance of the inflorescence or its maturation.

H. Spruceana—From the specimens it seems that the new flush is very slow in appearing after the inflorescence and that the fruit may be well along in its development before the new flush appears. Meanwhile, the previous flush leaves are very persistent. All inflorescence branches arise from the axils of the scales on the short-shoot (pl. 33, fig. 2).

H. rigidifolia—The previous flush leaves are very persistent until well after inflorescence maturation. From the few specimens at hand it is not possible to determine how long after inflorescence maturation the new flush makes its appearance. As above, all inflorescence branches arise from the short-shoot scale axils.

H. pauciflora—The previous flush leaves show a very strong tendency to persist until after the appearance and maturation of the inflorescence, as well as the appearance of the new flush which follows almost immediately after that of the inflorescence. Most of the inflorescence branches arise from the short-shoot scale axils but some may arise from the axils of the lower leaves on the new flush. A few specimens show a tendency for defoliation at the time the new flush makes its appearance. This may be due partly to removal of excess leaves by the collector (a frequent bad practice to "improve" the herbarium specimen) or it may be partly due to frequent hybridization with other species. The study of these characters in living material is especially critical in the *H. pauciflora* complex.

H. guianensis and varieties—A stronger tendency is shown for defoliation or partial defoliation preceding the appearance of the inflorescence than in *H. pauciflora*. Nevertheless, the majority of the specimens show at least a few leaves, particularly upper ones, remaining at the time the inflorescence appears and until the appearance of the new flush which shortly follows. Most inflorescence branches arise from the short-shoot scale axils. However, as in *H. pauciflora*, the upper inflorescence branches tend to arise from the axils of the lower leaves of the new flush.

H. nitida—This species is so very poorly represented in flowering material that little can be said except that some previous year's flush leaves (upper) tend to persist until after the appearance of the inflorescence. Although the basal inflorescence branches arise from the upper short-shoot scale axils, a greater number of the upper inflorescence branches arise from the leaf axils on the lower half of the flush.

2. Leaves not persistent on the previous year's flush, *i. e.* they abscise before the appearance of the inflorescence on that branch.

H. Benthamiana—Leaves are completely abscissed before the appearance of the inflorescence. The flush immediately follows the appearance of the inflorescence. The basal inflorescence branches arise from the uppermost bud-scale axils but mostly from the axils of the leaves on the lower two-thirds of the flush. A number of specimens, superficially resembling *H. Benthamiana*, show some persistent leaves, but close examination of the leaf, shoot and flower gives ample evidence that the specimens represent hybrids between *H. Benthamiana* and *H. pauciflora*, *guianensis* var. *lutea*, or *Spruceana*, from which the persistent leaf character probably is derived.

H. microphylla—Leaves are completely abscissed before the appearance of the inflorescence. Lower inflorescence branches arise from the upper bud-scale axils while the rest arise from the leaf axils of the lower third of the flush. However, on account of lack of sufficient material, the above observation may be somewhat inaccurate.

H. brasiliensis—Leaves are completely abscissed before inflorescence appearance. Lowermost inflorescence branches arise from the lowermost scale leaves of the flush and continue to arise from the axils of nearly all leaves of the flush except from a few of the uppermost ones[16].

[16]The fact that most axillary buds of the flush leaves have developed inflorescence branches may be of importance when it is necessary to bud graft material from the branches of mature trees. If such budding be necessary, as it is in selecting jungle trees for experimental and plantation use, one should choose so-called "corona" buds, those which occur in a rather crowded position near the terminus of the flush and from the inconspicuous short-shoot where no inflorescence branches likely have arisen.

It perhaps is of importance to note that the species falling in the first category showing persistent leaves are also those considered to have conspicuous short-shoots. Those of the second category with non-persistent leaves coincide with those species without conspicuous short-shoots. Although the character is used to a limited extent in the proposed key, I cannot as yet place full emphasis on it until further study has been made from living plants.

Leaflets: In a consideration of leaf characters as an aid to distinction of the various species one is forced to choose carefully and even then some overlapping can be expected. Although *Hevea* specimens usually are very large and difficult to collect, some leaflets may be found on the ground beneath the trees at any season. It is important, then, that we be able to derive maximum specific use from even a fallen, disintegrating leaflet and the aid of a pair of field glasses in determining an uncollectable forest giant from some area where *Hevea* has perhaps previously not been collected.

Position: Position of the mature leaflets with reference to the petiole axis is of prime importance in associating a particular plant within certain groups of species.[17] Two distinct contrasts may be found, *i. e.*: (1) Leaflets erect to slightly horizontal, in which case they stand up above the axis of the petiole to which they are attached. This type of position is found in the *H. guianensis* complex. (2) Leaflets distinctly horizontal to reclinate, the leaflets standing out in a plane parallel to that of the petiole or hanging down nearly perpendicular to the petiole axis. *Hevea brasiliensis* and *H. rigidifolia* are typified by reclinate leaflets while the remaining species are rather intermediate between horizontal and reclinate.

Lower lepidote surfaces: *H. nitida* is the only species in which scales are lacking or, at most, extremely sparse and sufficiently microscopic to produce a strikingly concolorous leaflet. All other species are characterized by having varying densities of minute, whitish, epidermal scales distinguishable with a strong hand lens. The presence of these scales accounts for the characteristic dull lustre and occasional whitish color of the lower surface. The scales are most densely disposed on the mature leaflets of *H. rigidifolia* and *H. pauciflora*, where they lie one against the other in tile-like regularity and are noticeably angular (hexagonal) in outline. In *H. Benthamiana* they are quite densely disposed but appear to be rather lens-shaped. In all other species they approach a circular outline, are more or less separated from one another, and vary in density from tree to tree. This specifically insignificant variation of density accounts for the description of a variety *subconcolor* under *H. brasiliensis*. This species shows a tendency for many individuals, throughout its entire range, to have relatively fewer, more widely spaced scales which in extreme cases would appear to produce the "subconcolor" condition.

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[17] Since this character is frequently hard to distinguish in herbarium material, it is advisable that collectors note it in their observations.

Pubescence: When present, leaflet pubescence is confined to the lower surface. In *H. Benthamiana* and *H. Spruceana* pubescence normally is found over the entire lower surface, associated with the veins and veinlets. In the former species it is usually reddish (occasionally mixed with whitish), while in the latter it is whitish.

In *H. guianensis* and *H. guianensis* var. *lutea* varying amounts of whitish or reddish-tinged pubescence normally are found associated with the midvein. In the latter the tendency is towards reddish or mixed reddish-tinged and whitish pubescence. In *H. guianensis* var. *marginata*, a slight whitish pubescence generally is associated with the midvein but may be harder to distinguish than in the previously mentioned members of the complex[18]. Type specimens of *H. pauciflora*, as well as those of *H. confusa* and *H. pauciflora* var. *coriacea*, all show very slight whitish pubescence associated with some portion of the midvein, usually within the upper half.

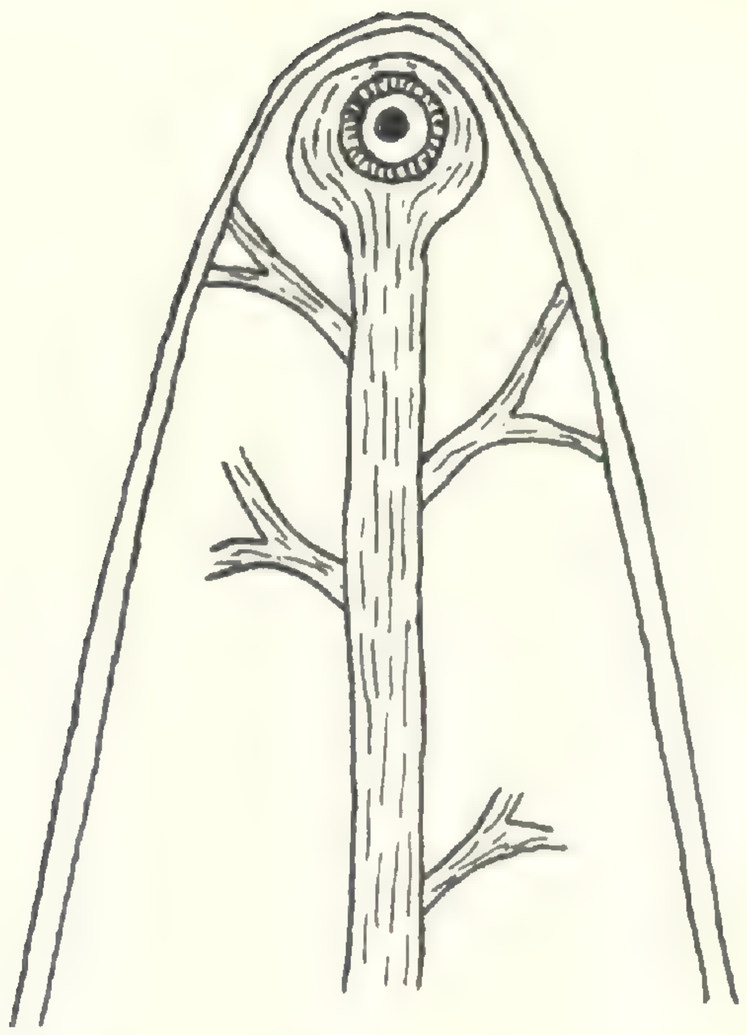
All the other species normally are without pubescence. Frequently, at least in *H. brasiliensis*, the very young leaflets may show some pubescence during the first days of their appearance. These minute hairs, however, soon are entirely caducous. Their presence or absence varies from plant to plant. There are specimens referable to *H. brasiliensis* in which pubescence can be noted along the midvein and even the lateral veins. Close observation, however, has given additional morphological evidence that they probably are introgressive hybrids.

Shape and Size: In many respects these features, especially the size, should be given very little significance. In the past, they have been responsible for perhaps more confusion and promiscuous varietal description than anything else. Size varies with the age of the plant; it varies from year to year depending on climatic conditions; and most noticeably it varies with the portion of the flush from which the leaves are taken. As a general rule, *H. microphylla* has the smallest leaflets within the genus, while *H. brasiliensis* produces some of the largest. It is not uncommon on any one flush of *H. brasiliensis* to find leaflets ranging in length from 5 cm. to 20 cm. or longer.

Shape at least is more constant for the individual than size. In general, *H. microphylla* has a narrow lanceolate leaflet, while *H. guianensis*, particularly var. *marginata*, tends toward an obovate outline. *H. pauciflora*, *brasiliensis* and *rigidifolia* usually have broadly lanceolate leaflets.

Leaflet Tips: Leaflet tips are a good character to use in distinguishing *H. rigidifolia* and *H. pauciflora*, which from sterile material alone frequently may be hard to tell apart. Rather voluminous material of *H. pauciflora* has failed to reveal a case in which the midvein extends all the way to the end of the blade tip. Furthermore, the end of the midvein always appears to be excised or calloused, and on mature leaflets produces a "socket" or glandular effect (text-fig. 3). This char-

[18] It should be stated that care must be exercised, particularly in the study of herbarium specimens, in distinguishing correctly between pubescence and simulated pubescence caused by hyphae and small fruiting bodies of certain minute fungi which protrude from the midveins. Apparently the veins form an excellent medium of fungus growth during the drying stage of the specimens.



Text-fig. 3. Leaflet tip on which the midvein terminates short of the blade tip and is glandular-calloused. Typified by *H. pauciflora*.

Text-fig. 4. Leaflet tip on which the midvein extends to the end of the blade tip and is not calloused. Typified by *H. rigidifolia*.

acteristic is unique in the genus. It is in strict contrast to *H. rigidifolia* where the midvein extends to the end of the long, narrowly acuminate blade tip, producing a cuspidate effect (text-fig. 4). In other species the midvein also extends to the end of the blade tip or even slightly beyond, as occasionally noted in *H. microphylla* and *H. brasiliensis*.

Texture: Hard coriaceous leaflets are found in *H. rigidifolia*. In *H. pauciflora* the leaflets appear to mature so slowly that a coriaceous condition can be expected only in the fully mature flush of perhaps several months of age. A coriaceous to subcoriaceous texture is the general rule for *H. guianensis* var. *marginata*, and to lesser extents in *H. guianensis*, *guianensis* var. *lutea*, *nitida*, and *Benthamiana*, especially when growing under poor soil and climatic conditions.

H. brasiliensis, *microphylla* and *Spruceana* are typified by membranaceous leaflets with considerable individual differences that are distinguishable as good clonal variations.

Margins: Revolute margins are the rule in *H. rigidifolia*. They are noticeable on the mature leaflets of *H. pauciflora* and form the main character in segregating the variety *marginata* from *H. guianensis*.

Inflorescence.—

The inflorescence arises from the terminal (occasionally axillary) bud regions of the young stems. It is composed of numerous panicles arising from the axils of the upper scales of the short-shoot. In a majority of the species panicles also arise from the axils of the lower scale leaves of the young flush and frequently from the axils of many of the flush leaves themselves. Under ideal growing condi-

tions trees will commence flowering when between three to five years old. Under forest conditions slow, competitive growth may prevent flowering until the tree is twenty to twenty-five years old.

The flowers of the inflorescence always are monoecious. The terminal flower of the primary and stronger secondary axes of the panicles is pistillate, all others being staminate. Flowering occurs normally once a year, following a dormant or wintering season during which some of the species defoliate completely, *H. brasiliensis* being an example. Other species, however, tend to flower without defoliation. Still others only partially defoliate or gradually defoliate during flowering or after subsequent flush development.

Thus far I have been able to make field studies on only two species with reference to inflorescence habits and their interesting relation to wintering (defoliation or non-defoliation), short-shoots, and the development of the flush. This inter-relationship between the various species is very strongly suggested by meager and incomplete herbarium collections from the Amazon valley, the assumption previously having been that these features are the same in all species. It does appear that a complete comprehension of the genus will be aided materially by a full understanding of the inflorescence and its habits for the different species; a summary of which is suggested under the discussion of leaf persistence.

Buds and Flowers: Sketches of both male and female buds and flowers of each important taxonomic entity of the genus are presented in pls. 35, 36, 37, 38, and 39.

The flowers, though small and difficult to dissect, are relatively easy to study after one has mastered the fundamentals of their morphology. With the key here proposed, microscopic dissection of the flower rarely seems necessary, and then only for critical study. Usually sufficient characters may be seen from the superficial bud and flower aspects to make more technical observations unnecessary.

The staminate flower has a short pedicel subtended by a small caducous bract, in the axil of which usually an abortive bud is found. After anthesis the flower abscisses from the peduncle. The perianth is composed of a short calyx tube and five valvate lobes. Petals are absent but a disk is present which may be represented merely as a slight swelling or enlargement of the base of the staminal column, by the presence of five gland-like protuberances, or by five relatively large petal-like acute lobes which seldom reach farther than to the lowest anthers. The anthers range from five to ten in number. They are sessile and attached in one regular or irregular, two irregular, or two regular whorls on a staminal column. The staminal column represents the fused filaments in conjunction with the rudimentary pistil, the tip of which extends beyond the anther whorls and may or may not be slightly lobed or divided giving a stigma-like impression.

The pistillate flower has a somewhat longer pedicel than that of the staminate and likewise abscisses from the peduncle unless it be successfully fertilized. The pedicel dilates into a torus which is conspicuous only in the case of *H. microphylla*.

Here again the perianth is composed of calyx tube and five valvate lobes. Contrary to the habit of the staminate flower, the tube abscisses after anthesis at its point of junction with the torus. Neither petals nor stamens are present but a conspicuous or inconspicuous disk is found. In some cases it is possible to distinguish between petal-like and stamen-like disk lobes. The pistil is present in the form of a trilocular, tricarpellary ovary, each cell of which has but one ovule. The three stigma lobes may be entire or somewhat lobed and are sessile, though in rare cases they may be very shortly stipitate.

Color: With the exception of *H. Spruceana,* which normally has a dark reddish purple to purplish brown calyx tube, all the species have flowers which are uniformly cream-yellow to brownish yellow in color.

Pubescence: Variation in floral pubescence appears to be of some significance in speciation. In general, the species of *Hevea* have their buds and flowers covered with very short whitish hairs. In *H. Benthamiana* these hairs not only are longer than in other species but have a distinctly reddish color. Within *H. guianensis* and its variety *lutea* there frequently is a reddish tan cast to the short floral pubescence, while the color of the hairs on the peduncles and pedicels tends to be more reddish in tinge. At the point of contact between the peduncle and pedicel there appears to be a narrow band of longer, more dense hairs which is noticeable in *H. Benthamiana, guianensis* and varieties, and *rigidifolia.*

The staminate buds and flowers in all species appear to be rather uniformly pubescent without. The pistillate flowers of four species, however, show remarkable variation. *H. pauciflora,* having pubescent lobes without, is distinctly glabrous below the lobes on the tube and well on the pedicel. *H. microphylla* becomes conspicuously less pubescent on the tube below the lobes and has a glabrous torus and pedicel. The lower-center portion of the lobes of *H. nitida* become glabrous as well as the tube. *H. brasiliensis* is slightly less pubescent on the tube than on the lobes. All other species appear to have uniformly pubescent lobes and tube.

The inner surface of the calyx lobes apparently is somewhat pubescent in all the species, the pubescence being conspicuously longer in *H. pauciflora.*

The ovary, although characteristically short-pubescent or somewhat silky throughout the genus, is definitely glabrous in *H. microphylla* and *H. rigidifolia.* In both *H. pauciflora* and *H. nitida* there is a tendency towards glabrescence.

Calyx Lobe Acumination and Lobe Tips: Bud shape, particularly as to whether it be obtuse or acuminate, has been frequently used as a taxonomic character with special reference to the staminate flower (Huber, 1906). The illustrations (plates 40 and 41) will show the importance of the degree of acumination with reference to the calyx lobes of the mature flower as well as the bud. It should be noted that the degree of bud acumination is not always indicative of the degree of mature calyx lobe acumination; furthermore, that the degree of bud and lobe acumination is not always the same for both the male and female flowers.

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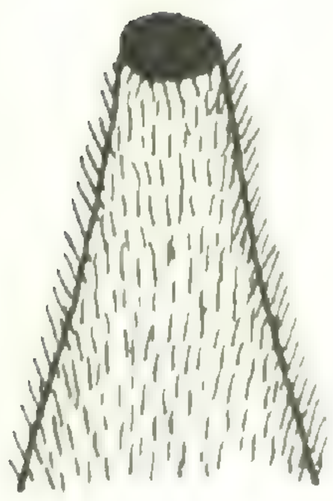

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Text-fig. 5. The normal calyx lobe which is acute and pubescent to the tip.

Text-fig. 6. Calyx lobe which is bluntly acute, calloused and glabrous at the tip. Found conspicuously in *H. pauciflora* and *H. nitida*, and less well developed in *H. brasiliensis*.

Two other characters, neither of which appears to have been noted previously, are of importance when taken with the consideration of acumination: (1) Shape of the lobe tips (pl. 43, figs. 1-2), *i. e.*, whether they be acute and pubescent as shown in text-fig. 5, or whether they be blunt and glabrous (calloused) as shown in text-fig. 6. Calloused calyx lobe tips of both staminate and pistillate flowers are found in *H. pauciflora* and *H. nitida*, and to a less pronounced degree in *H. brasiliensis*. (2) The absence or degree of contortion of the bud tip and resulting mature lobes. Contortion in its most pronounced degree is found in both the staminate and pistillate flowers of *H. rigidifolia* (pl. 43, fig. 3) and to a lesser degree in *H. brasiliensis* and *H. microphylla* (pls. 38-39).

Disk: The disk, both in staminate and pistillate flowers, is a rather conspicuous feature of the genus *Hevea*. It is of taxonomic significance when its development in the various species is compared (see pl. 42). The disk of the staminate flowers appears to represent petals. When lobes can be distinguished their position alternates both with that of the calyx lobes and the anthers of the lower whorl. In the pistillate flower a study of the disk lobes, where conspicuously present, indicates the disk to represent both petals and stamens. Frequently the petal-like lobes alternate with structures which appear to be much-reduced stamens, both filaments and anthers being distinguished. Most frequently the disk lobes are attached to the base of the ovary, but cases have been noted in dissections where they are slightly adherent to the calyx at the point of its abscission.

Like other characters, the disk developments are inclined to show a great deal of transition from one extreme to the other from one to the next species. As in the case of acumination, the same degree of development does not always carry through in a parallel fashion between the staminate and pistillate disk of the same species.

Torus: Morphologically all of the species of *Hevea* can be considered to have a torus in the pistillate flower (pls. 41-42). It is only in *H. microphylla* that it is so pronounced (pl. 43, fig. 2) that it may be used immediately in distinguishing that species from all others. Though not a conspicuous character in the genus, it is rather well developed also in *H. pauciflora*.

Anthers: Each stamen consists of a bilocular, longitudinally dehiscent anther, sessile or nearly sessile and attached directly to the staminal column (see upper figures, pl. 42). The column is composed of fused filaments as well as the rudimentary pistil. This accounts for the columnar portion extending above the anther whorl or whorls and explains why this staminal column tip frequently is found to be so variable within the species, *i. e.*, it may be acute, blunt, long, short, entire, bi-lobed or even tri-lobed.

In taxonomic studies of *Hevea* considerable stress has been paid to anther number, on the basis of which two sections, *Eubevea* Muell.-Arg. and *Bisiphonia* (Baill.) Muell.-Arg., were erected by Mueller-Argoviensis (1865). Through a study of more complete material I have arrived at the opinion that exact number of anthers is of little taxonomic significance within the limits of certain tendencies. These tendencies are towards 5 anthers in one whorl as typified by *H. guianensis* and its variety *marginata;* towards 6–8 or 9 anthers in two irregular whorls in which the upper is the more irregular, as found in *H. guianensis* var. *lutea, Benthamiana,* and occasionally in *Spruceana, pauciflora,* and *rigidifolia;* and towards 10 anthers in two regular whorls of which *H. brasiliensis, nitida* and *microphylla* might be considered typical. However, the number of anthers may vary within the species and between flowers on the same tree. As is to be expected, if there be two whorls, the anthers of the upper alternate in position with those of the lower.

An anther character of perhaps considerable significance, and one not previously stressed, is the size. Anthers within the genus appear to fall into two definite size groups, those which approach 1 mm. in length and those of about 0.5 mm. in length, with no definite recognizable gradation. The nearest approach is in *H. guianensis* var. *lutea,* where both sizes frequently are present in the same staminate flower, but with little size gradation one into the other. So far as I am able to determine, the large anthers are associated only with the *H. guianensis* complex. They appear quite uniformly in the predominant number of 5 in one whorl in both *H. guianensis* and its variety *marginata.* In all other species the anther size approaches 0.5 mm. with the exception of *H. guianensis* var. *lutea* where both sizes may sometimes be present (usually only one or two of the large size). However, it must be remembered that this is an extremely variable and transitional variety in which frequently none of the larger anthers are present on the irregular whorls, but if present are on the lower whorl.

Fruit.—

The fruits are disposed terminally on the inflorescence branches but the ratio of developed fruits to the total number of female flowers is perhaps only one to ten or twenty. So far as I know, the fruit of all species tends to hang down due to its weight on the peduncle. Because of the comparatively long inflorescence in both *H. brasiliensis* and *H. pauciflora,* and because the terminal pistillate flower tends to be the one which most frequently develops fruit, the peduncles of these two species seem to be longer than those of the other species, and of course droop more. The departure of the peduncle from the branches of *H.*

pauciflora is conspicuous in that it is at a right angle, after which rather sudden drooping occurs. In *H. brasiliensis* and other species, the peduncle departs from the branch at considerably less than a right angle and droops in a more gradual arc.

The fruit is quite uniform throughout the genus, normally being a 3-carpellary dehiscent capsule of relatively large size. The carpels are bivalved, composed of a coriaceous pericarp and a woody endocarp which varies in thickness with the species. Each carpel normally contains one seed. In some trees, particularly noted in plantings of *H. brasiliensis*, the capsules are occasionally 4-, or even 5-, carpelled, all carpels containing a normal, viable seed. Perhaps through abnormal or imperfect fertilization, capsules sometimes mature normally in every respect except for the seeds, which may be rudimentary or abortive in one or more of the carpels.

Three distinct variations in the capsule of *Hevea* occur: (1) The most prevalent type is subglobose in outline with more or less emarginate, mucronate tip. In cross-section, it is distinctly 3-lobed. In dehiscence this type is violently explosive, both the seeds and capsule parts being thrown as much as 15–20 meters. All that remains on the tree is the peduncle and placenta. There appears to be considerable variation in the thickness of the woody capsule walls or endocarp between species with this type of fruit. *H. guianensis* and its varieties, *H. brasiliensis*, *nitida*, and *pauciflora* tend to have a thick, woody endocarp in which the valves retain their original shape with little noticeable contortion. On the other hand, *H. Benthamiana* and *H. rigidifolia* have a relatively thin, woody endocarp, the valves of which show very noticeable contortion at dehiscence, especially *H. rigidiflora*. (2) The fruit of *H. microphylla* is unique in that its shape is pyramidal, tending toward an acute apex, and is noticeably keeled. The carpel walls are thin and leathery, being composed of a coriaceous pericarp and an almost paper-thin, woody endocarp. Dehiscence is not explosive; rather, the valves appear to open slowly, greatly contorting and allowing the seeds merely to fall. The valves appear to be persistent to the receptacle for a considerable time after dehiscence; the torus of this species is very conspicuous at the base of the fruit. (3) The fruit of *H. Spruceana* likewise is unique for the genus in that it is much larger, ellipsoid to subovoid, obtuse at the tip, and round in cross-section. The carpel walls are composed of the coriaceous pericarp and a very thick, woody endocarp. Although dehiscence is somewhat explosive, there is little contortion of the valves, and they are persistent to the receptacle for some time. The seeds are not thrown far.

Seeds: Hevea seeds[19] are similar in shape and color patterns to those of the castor bean, *Ricinus*, but they are, with few exceptions, very much larger and they always lack the persistent caruncle in mature condition. Reserve material has a very high percentage of oil. Length of viability is normally only a few weeks. Exposure to full sun and drought will shorten this period, while packing in a cool,

[19] Wild pigs, Peccary, of which two common types are known locally in Peru as *huangana* and *sajino*, are extremely fond of the seeds. Deer, *venado*, appear to relish the young seedlings coming up under the trees. Wild game is particularly abundant during the *Hevea* seed season, augmented by many members of the Cat family which prey on both the wild pigs and deer.

slightly moist medium can extend it to two or three months. Although abundant moisture and deep shade is essential for seed germination, the young seedlings soon perish if not exposed to rather full sunlight. Various types of seed twinning have been reported but this seems to be rare.

Much consideration has been given to the color patterns of the outer seed surface of *H. brasiliensis* (La Rue, 1919) as a means of identifying individual trees within the species. Color patterns are relatively stable for the individual. It would appear that coloration is of little use in speciation, with the possible exception of *H. Benthamiana,* where the background is light in comparison with the more tannish background of other species. The brown mottling, too, appears to be somewhat clearer and more brilliant than in other species.

Over-all seed size is apt not to be constant, except in *H. Spruceana,* which is longer than any other species. In this connection the length/thickness ratio is the important factor, seeds of *H. Spruceana* being at least twice as long as thick while in all other species the length is less than twice the thickness.

Shape of the seed, especially in cross-section, tends to be relatively constant for the species and can give considerable aid in speciation. The following generalizations may be made regarding shape and other seed tendencies as an aid to species determination:

H. Spruceana.—Several unique characters are present in the seeds. They are at least twicè as long as thick, in contrast to those of all other species whose length is less than twice their thickness. The longitudinal-section through the dorsiventral plane shows a slight curved (approaching reniform) condition, suggesting a similarity in both shape and size to the kernel of a Brazil-nut. In cross-section, the seed is sharply angled in that the compressed flattened ventral and the two lateral angles formed at the junction between dorsal and ventral surface are very prominent. The dorsal surface tends to be uniformly rounded with a rather faint dorsal angle.

H. microphylla.—The seed is unique. It is triangular-ovate in outline, with the smaller end the micropylar end.

H. brasiliensis.—Seeds normally are ellipsoid in outline, somewhat compressed on the ventral surface. In cross-section, the dorsal surface tends to be uniformly rounded, as does the more flattened ventral surface. If any angulation is present it is seen at the junction of the two surfaces. It appears that the presence of germ-plasm from other species will produce noticeable effects on the angulation or generally rounded condition.

H. Benthamiana.—In general, this species has smaller seeds than *H. brasiliensis* but, like in that species, they tend to be quite rounded. In color, they have the noticeably whitish background and brilliant brown spots in contrast to the tannish background of other species. Here again hybridization, or at least presence of germ-plasm from other species, seems to produce pronounced effects on the shape.

H. guianensis and its varieties.—The seeds tend to show a distinctive 4-angled cross-section in which the dorsal sides are longer than the ventral sides, producing a kite-shaped effect. Each side of both the dorsal and ventral surfaces shows a shallow concavity running throughout most of the seed length.

H. pauciflora and *H. rigidifolia.*—The seeds show a decided hexagonal cross-section in which two sides are on the ventral surface and four sides make up the dorsal surface. Each of the dorsal sides tends to have a shallow concavity running nearly the entire length of the seed. On the ventral surface the two sides form prominent lateral concavities on the upper two-thirds of the seed but this is replaced by a central concavity on the lower third.

H. nitida.—Seeds of this species appear to have the upper half of the ventral surface composed of two lateral concavities, replaced by one larger, central concavity on the lower half. On the dorsal surface there are two shallow concavities. In the cross-section of the micropilar end a 4-angled, kite-shaped effect is produced which is not noted in the basal cross-section. Not enough seeds of this species have been seen on which to base an accurate description.

POLLINATION

Very little is known regarding the pollination of *Hevea* in nature. Since the pollen grains are rather sticky, wind can be eliminated as a factor. Ramaer (1935), in certain hand-pollination experiments, found that cross-pollinations were considerably more successful than self-pollinations. Workers in *Hevea* consider that cross-pollination is the rule, but cases are known where a tree isolated from other trees by many miles repeatedly set fertile fruit year after year. There are other cases, particularly in isolated mono-clonal plantings, where certain clones will not set fruit unless planted in close proximity to other clones. The fact that *Hevea* has set fruit wherever it is planted and comes into flower might indicate that no highly specialized insect adaptation is necessary for its pollination. The terminal position of the pistillate flowers on the inflorescence and its major branch axes could indicate that cross-pollination by flying insects might be favored.

One never can find a jungle *Hevea* tree in bloom that is not covered with ants, usually of varied species, including leaf-cutters, occasionally carrying the flowers to their nests. Though ants cannot account for cross-pollination, they may be an important factor in selfing. Maas (1919) states that members of the Nitidulidae, Phlacridae, small Curculionidae, fly species and small bees, have been seen on *Hevea* flowers in the Far East. I have observed the common Honeybee to frequent the flowers of *Hevea* growing at the Plant Introduction Station, Coconut Grove, Florida, but little, if, any, reference has been made regarding the possible pollinators in the natural habitats.

Since we find that natural hybridization is taking place among the species in the Amazon valley, it is imperative to know something of the conditions of cross-pollination and what insects might account for it. *H. brasiliensis*, at least, tends to open its flowers during the latter half of the afternoon but pollen is said to be fertile only for perhaps a day, losing its viability rather rapidly in dry sunny weather (Maas, 1919). The pistillate flower apparently is receptive for two to three days. In view of this, both day- and night-flying insects must be taken into consideration. It would appear that conditions for successful cross-pollination, where species are separated by distances of a mile or less, would be best at night. Within the Peruvian range of *Hevea*, species of stingless bees, both *Melipona* and *Trigona*, have been seen in abundance around and on flowers of *Hevea*. *Melipona*, especially, remains on the flowers even after the felling of a branch. Little seems to be known regarding the distances traveled by members of these genera, but Michener (1946) has made such observations in Panama. It would appear that these stingless bees tend to concentrate on a few trees and work within comparatively limited ranges, accounting mostly for selfing. Dr. Herbert F. Schwartz, of the American Museum of Natural History (correspondence Feb. 5, 1947), has suggested that members of the Megalopta bees (Halictidae) might account in part for the night-flying insects visiting *Hevea*. He has identified a specimen of this group taken from a *Hevea* flower as a species of *Augochlora*. Besides the bees, wasps also are frequent visitors of *Hevea* trees in flower, the nests often being encountered.

At the present time, there appears to be more positive evidence that selfing may be the rule under jungle conditions. Here trees, even of the same species, may be separated by a relatively few meters or up to a kilometer or so. Nevertheless, it must be pointed out that we scarcely know anything of the upperstory fauna in tall forest trees even during the day, much less at night.

Cytological Summary

According to Baldwin (1947), all the species of *Hevea* thus far studied cytologically have a normal 2n chromosome count of 36, confirming the work of Ramaer (1935), Paddock (1943) and Perry (1943). Baldwin found one individual of *H. pauciflora* to have 18, and another of *H. guianensis* var. *marginata* with 54. Perry (1942) states that "all *(Hevea)* species studied are tetraploid." Ramaer (1935) considered 18 chromosomes as the basic 2n number for *Hevea*. Baldwin believes the normal 36 2n chromosome number likely to be tetraploid, and that the individual with a 54 2n number probably is hexaploid.

Intraspecific Variation

Some excellent research has been carried on at Far Eastern experiment stations concerning morphological variations of trees of *H. brasiliensis*. No part of the plant's anatomy seems to be without its range of intraspecific variation (Frey-Wyssling, 1931, 1933; Frey-Wyssling, Heusser and Ostendorf, 1932; Assoc. Cent. Exp. Sta., 1939). Furthermore, Bobiloff (1931) has brought out that there are physiological differences between clones of the same species with regard to latex color reactions through the addition of calcium chloride. More recent work is dealing with variations in individual susceptibility to diseases, being carried on by Langford (1945).

Casual observations sometimes lead one to feel that there are more differences between two trees of the same species than between two species. This is especially true when the observer is highly familiar with the details of many clones of *H. brasiliensis* but not with the other species.

My own preliminary observations, as well as those of previous workers, indicate that there is a tendency towards opposing extremes in any one morphological variation; but since the extremes are probably based genetically on multiple factor differences, there are always intermediates present. It also has been observed that though one or many characters may be intermediate in nature, there are other characters which more closely approach one or the other extreme of the total expected variation. A list of variable intraspecific characters can be of material aid in tabulating ranges of variation within species. Large-scale scoring of intraspecific variations, in comparing species, would show amounts of parallel variation ranges between species; and may eventually be used, when more material is available, in showing that a number of species grade one into the other.

Speaking from a more practical standpoint, intraspecific variations are of great value in distinguishing *Hevea* clones. The proper identification of young, sterile,

bud-grafted material or clones in the field planting, budwood garden, and experimental plot is of utmost importance since mixtures due to lack of careful supervision and other unavoidable factors frequently occur and, if not detected, can lead to high production losses.

For the relatively few clones in commercial use in the Far East, the written descriptions amply have served their purpose, even without the actual devising of keys for their identification. The cooperative Hevea Plantation Improvement Program, being carried on by the U. S. Department of Agriculture in cooperation with many of the Latin American countries and commercial rubber companies, has resulted in the amassing and distribution of hundreds of *Hevea* clones selected from superior jungle trees. It also has resulted in the selection of thousands of nursery seedlings from various seed progenies collected throughout the Amazon valley, and is resulting in thousands more of hand-pollinated crosses, all of which are undergoing experimental tests. Once these individuals are proved resistant to strains of the South American Leaf Blight, *Dothidella Ulei,* both under natural and artificial innoculation, they must be distributed to various experiment stations and cooperators for field trials. With each move and each distribution, the chances for an error in labelling increases many-fold.

A comprehensive study of individual morphological variations and their consistency for use in the accurate identification of many clones will in itself be a long-time work. It will be one in which frequent revisions and changes will have to be made to keep abreast of the advancing development and introduction of more and more proved clones into commercial use. The work at first will be largely devoted to the use of vegetative characters to be found on the young budded plants. From this, it will advance to include characters of the mature tree, as bark, latex, trunk and branching. Finally, it must include variations in inflorescence, flower, fruit and seed, which, though not so important for the planter, are necessary for the geneticist and plant breeder.

In making up preliminary lists of intraspecific variable characters, I have, of course, drawn heavily from the previous work on clone characters; but in working with and selecting jungle material and subsequently studying it as young buddings in nurseries, many additional variations have come to my attention. Such would be expected since the new material is coming from widely separated localities and from the jungle instead of from the original stock on which the Far Eastern industry is based. Certainly many other contrasting characters are yet to be observed, and one can readily see that all possible combinations of the many character variations would lead to astronomical figures. There is little reason to doubt that keys could be devised to take care of any number of clones desired to be identified.

The most practical means of large-scale clone identification would not necessarily have to be in the form of a key. The punch-card system might better be adopted in which only combinations of strongly contrasting characters be used, disregarding all intermediates.

The following intraspecific characters are listed with their contrasting conditions which have been found to exist within *H. brasiliensis*. Since the greatest practical need for intraspecific variations lies in the differences on young budded clones, the characters found on young, sterile plants are stressed. I have had little opportunity for practical observation of characters of this sort from large progeny numbers of species other than *H. brasiliensis*, or, for that matter, of many of the known interspecific hybrids. Yet from some such observations made on *H. guianensis* var. *lutea* there is reason to believe that parallel conditions exist in other species. With little revision, these lists of intraspecific variations might well apply to the hybrids as well as the species, after the material in question has been given its proper specific rank.

TRUNK (STEM)—
- GROWTH: strong or weak
- FORM: erect or leaning
- BASAL CROSS-SECTION: round or fluted
- BARK
  - GREEN: with or without bloom
  - BROWN-GREEN
    - LENTICELS: conspicuous or inconspicuous
      - COLOR: whitish or as cork
    - FIRST CORK: on flush or on interflush
      in streaks or in spots
  - BROWN
    - COLOR: grayish, tannish, reddish or brownish
    - LENTICELS: conspicuous or inconspicuous
      - SIZE: large or small
      - COLOR: whitish or as cork
      - CORK: smooth or rough
        - GROWTH CRACK INTERVAL: fine or coarse

LATEX
- COLOR: white, cream or yellow
- CONSISTENCY: watery or thick

BUDS[20]
- TERMINAL
  - BUD SCALES: few or many
    - SHAPE: linear or deltoid
- AXILLARY: depressed or exserted; early-sprouting or late-sprouting

LEAF SCAR: protruding or not protruding
- MARGIN: protruding or not protruding

STIPULES: conspicuous or inconspicuous
early caducous or late caducous
- SHAPE: linear or deltoid

TYPICAL FLUSH
- SHAPE: asymmetrical or symmetrical
  half-globular or globular segment
  conical or truncate-conical
- DIMENSIONS: large or small
  broad or narrow
  tall or short
- DENSITY: sparse or dense
- STORIES: continuous or separated

LEAVES—
- PETIOLES: longer or shorter than blades
  - DIRECTION: downward, horizontal, or upward
  - FORM: straight, arcuate, inverse-arcuate, or sigmoid

[20] Bud characters could be substantially augmented when considering other species in addition to *H. brasiliensis*.

BASE: normal or much swollen
suberized or not suberized
DIMENSIONS: long or short
thick or thin

PETIOLULES
ANGLE BETWEEN EACH: broad (above 90°) or narrow (below 70°)
DIRECTION: downward, horizontal, or upward
FORM: clawed or not clawed
SIZE: long or short

LEAF BLADES
COLOR: yellowish green, light green, or dark green
PUBESCENCE[21]: absent or present on veins
UPPER SURFACE LUSTRE: glossy or dull
LOWER SURFACE LUSTRE: subconcolorous or not subconcolorous
TEXTURE: membranaceous or coriaceous
SHAPE: lanceolate or oblanceolate
ovate or obovate
diamond or rhombic
suborbicular (orbicular leaflets have not yet been noted)
SIZE: large or small
MARGIN: plane, wavy or crisped
revolute or not revolute
MIDVEIN: terminating short of blade tip, extending to end of blade tip, or extending beyond blade tip
LATERAL VEINS: continuous, forked or branched
TIP: OBTUSE: attenuate (acuminate) or short (not acuminate)
ACUTE: acuminate or not acuminate
BASE: acuminate or not acuminate
obtuse or acute
LONG-SECTION PROFILE: flat or convex
CROSS-SECTION PROFILE: flat, V-shaped or boat-shaped
POSITION TO PLANE OF PETIOLE: erect, semi-erect, parallel, declined or horizontal
POSITION TO EACH OTHER: apart, touching or overlapping

MISCELLANEOUS ABNORMALITIES
LEAVES: more than 3 leaflets
less than 3 leaflets
leaflets concrescent

The above intraspecific variations are but a few when considering that these are found in the young plant. An over-all consideration of the mature trees would include not only the above but would be augmented by many more, some of which have been mentioned under the morphological discussions. A few of the more pronounced intraspecific variations of mature trees may be found in the nature of the corky bark surface, its color, and its method of exfoliation. The color of the phloem is highly characteristic, and five color divisions already have been mentioned. The nature of the branching also can be placed in various classes. Besides the study of variations in seed-color pattern, very little has been done regarding intraspecific variations in the inflorescence, flowers, floral pubescence, fruit and seed shapes, all of which show innumerable variable contrasting characters. However, as yet they are not sufficiently well studied to be presented in this paper.

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[21] In considerations including other than *H. brasiliensis*, pubescence characters can be greatly augmented and highly significant.

KEY TO THE PRINCIPAL SPECIES AND VARIETIES OF HEVEA

A. Leafy shoots (flushes) alternating with relatively elongate, caducous-scaly short-shoots[22] (interflush short-shoots[23]).
  1. Leaflets distinctly erect to slightly horizontal[24]; staminate flowers without disk lobes; seeds with 4-angled (kite-shaped) cross-section.
    a. Staminate buds broadly obtuse to rounded (may be somewhat acute in var. *marginata*); anthers about 1 mm. long, normally 5 in one whorl.
      α. Leaflets membranaceous to subcoriaceous, not revolute..... 1. H. GUIANENSIS[25]
      β. Leaflets coriaceous, revolute..... × *H. guianensis* var. *marginata*
    b. Staminate buds acute to acuminate; anthers about 0.5 mm. long (one or more may approach 1 mm.), normally 5–7 in two irregular whorls..... 1a. H. GUIANENSIS var. LUTEA
  2. Leaflets distinctly horizontal to reclinate; staminate flowers with disk lobes; seeds variously shaped.
    a. Leaflets concolorous, not lepidote on the lower surface; leaf flush tending to defoliate before appearance of inflorescence, at least before appearance of new flush; staminate disk lobes very conspicuous, attaining lower whorl of anthers..... 2. H. NITIDA
    b. Leaflets not concolorous, densely whitish-lepidote on the lower surface; leaf flush usually persistently leafy until after inflorescence maturation and appearance of new flush; staminate disk lobes inconspicuous, short.
      α. Mature leaflets coriaceous, glabrous below; flowers yellowish; diameter of staminate flowers normal for the genus (about 2.5–3 mm.); pistillate disk lobes conspicuous, long-acute; fruit with 3-lobed cross-section; seeds hexagonal in cross-section, length less than twice the thickness.
        I. Leaflets conspicuously revolute, hard-coriaceous, cuspidate, midvein extending to end of blade tip, not callose-tipped; staminate buds long-acuminate, conspicuously contorted; calyx lobes acute-tipped, pubescent to tip, not calloused.... *H. rigidifolia*
        II. Leaflets not conspicuously revolute, membranaceous when young, becoming coriaceous with slow maturation, not cuspidate, with midvein terminating before reaching blade tip, having a glandular, calloused tip; staminate buds obtuse, never contorted; calyx lobes blunt-tipped, the tips calloused, glabrous..... 3. H. PAUCIFLORA
      β. Mature leaflets membranaceous, usually noticeably whitish-pilose over entire lower surface; flowers reddish to brownish purple, at least the calyx tube; staminate flowers largest in diameter for the genus (about 4.5 mm.); pistillate disk lobes inconspicuous; fruit with round cross-section; seeds ventrally compressed-angular, otherwise, rounded in cross-section, length at least twice the thickness..... *H. Spruceana*

B. Leafy shoots (flushes) alternating with narrow rings of bud-scale scars[26] (interflush rings)[27].

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[22] Refer to text-fig. 1 and pl. 32, fig. 2.

[23] Attention is called to cases where hybridization between species of this group and those in which the short-shoot is not conspicuous has produced rather rare individuals, though otherwise characteristic for the most part of one of the short-shooted species which may not have this feature in evidence.

[24] Position of leaflet frequently of little use in the herbarium.

[25] Species printed in capitals are those represented in Peru; those printed in lower case have not been found to occur in Peru.

[26] Refer to text-fig. 2, and pl. 32, fig. 1.

[27] Attention is called to cases where hybridization has occurred with conspicuously short-shooted species, the short-shoot being usually conspicuous in the hybrid. As is particularly evident in *H. Benthamiana* hybrids, the specimen may superficially resemble that species in most characters except a conspicuous short-shoot.

1. Leaflets usually reddish-pilose over entire lower surface; anthers normally less than 10 in two irregular whorls; seeds showing distinct whitish background under brilliant, clear brown spots.....4. H. Benthamiana
2. Leaflets glabrous below; anthers normally 10, in two regular whorls; seeds showing distinctly tan background under usually dull brown spots.
   a. Leaflets relatively small (5–12 cm. long); flowers very long (staminate about 7 mm.; pistillate about 11 mm.) for the genus, the pistillate with an enlarged torus; calyx lobes acutely acuminate, pubescent to tip, not calloused; both staminate and pistillate disk lobes small but conspicuous; ovary glabrous; capsule pyramidal, acute; valves thin, leathery; seeds triangular-ovate in longitudinal section..... *H. microphylla*
   b. Leaflets relatively large (5–30 cm. or more long); flowers of median length (staminate 5 mm.; pistillate 8 mm.) for the genus, the pistillate without an enlarged torus; calyx lobes bluntly acuminate, with small calloused, glabrous tips; both staminate and pistillate disk lobes very small and inconspicuous; ovary silky-pubescent; capsule subglobose, emarginate; valves thick, woody; seeds oval in longitudinal section.....5. H. brasiliensis

The Peruvian Species

1. Hevea guianensis Aubl. Hist. Pl. Guiana Fr. **2**:871. (*pl. 335* as *H. peruviana*, sphalm). 1775.

Jatropha (?) *elastica* L. Sp. Pl. Suppl. 422. 1781.
Caoutchoua elastica (L.) H. F. Gmel. Syst. 1007. 1791.
Siphonia Cahuchu Rich. ex Willd. Sp. Pl. **4**:567. 1805.
Siphonia elastica (L.) Pers. Syn. Pl. **2**:588. 1807.
Siphonia guianensis (Aubl.) Juss. Euphorb. Gen. 40 (*pl. 12, fig. 38a* as *Siphonia elastica*, sphalm). 1824.
Hevea nigra Ule, in Engl. Bot. Jahrb. **35**:667. 1905.
Hevea caucho Posada, Estudios Cient. 212. 1909, nom. nud.
Hevea collina Huber, in Bol. Mus. Goeldi 5:249. 1909.
Hevea guianensis var. *collina* (Huber) Ducke, in Archiv. Jard. Bot. Rio de Janeiro 4:109. 1925.
Hevea guianensis var. *cuneata* (Huber) Ducke, l. c. **6**:51. 1933, in part.
Hevea guianensis ssp. *occidentalis* Ducke, in Archiv. Inst. Biol. Veg. Rio de Janeiro **2**:229. 1935.
Hevea guianensis var. *occidentalis* Ducke, l. c. 1935.
Hevea guianensis ssp. *typica* Ducke, l. c. 227. 1935.

Medium-sized to large tree to 40 m. tall; trunk cylindrical; branches somewhat reddish; short-shoots very conspicuous, of somewhat greater diameter than the long-shoots; bud scales very numerous, linear, about 6 mm. long, early caducous. Leaves partly persistent until after appearance of inflorescence; mature leaflets erect, membranaceous to thinly coriaceous, usually obovate with short acuminate tip, the pubescence of sparse hairs on lower surface along midvein, tannish or somewhat reddish, the scales of the lower surface roundish, the midvein continuous to end of blade tip, not calloused. Flowers yellowish, staminate buds rounded to obtuse, not contorted, the short pubescence whitish-tan to reddish, rather uniformly distributed except at abscission region of pedicel where the hairs are more dense and longer; staminate flowers about 3.5 mm. long and 3 mm. broad, the calyx lobes acute and acute-tipped, not calloused and not acuminate, the disk inconspicu-

ous, represented by a slight flaring of the staminal column base, the anthers normally 5, approximately 1 mm. in length, in one whorl; pistillate buds obtuse to acutish, not contorted, the pubescence short, uniformly whitish tan to reddish; pistillate flowers about 6 mm. long and 3 mm. broad, the calyx lobes acute and acute-tipped, not calloused, scarcely acuminate, the disk inconspicuous, the ovary silky-pubescent. Fruit maturing green in color, subglobose, emarginate-apiculate with 3-lobed cross-section; capsules ligneous, explosive, the valves thick, showing no contortion at dehiscence; seeds quadrangular-kite shaped in cross-section, to about 20 mm. long and 18 mm. thick, latex sulphur to cream-yellow; rubber and yield rather inferior.

VERNACULAR NAMES: *shiringa debil, jebe debil* (Peru).
KNOWN NATURAL DISTRIBUTION: Upland forests of the Guianas, Venezuela, Colombia, Brasil and eastern north-central Peru.
PERU: DEPT. LORETO: Rio Napo, Clotilde, fl.[28] Sept. 1940, *Skutch 4985*.

Hevea guianensis in pure strain appears to have been collected rarely in Peru. Ducke has collected it (No. *1433*, Feb. 2, 1942) from near the mouth of the Rio Yavari on the Peru border, and various collections are reported from the Colombian border on the Rio Putumayo. It appears to reach its western limits on the low *tierra altura* hills on the Rio Napo, extending into the vicinity of Iquitos where collections indicate it to exist in forms contaminated with *H. pauciflora*. Other collections, as the type of *H. nigra (Ule 5895)*, from the upper Rio Jurua, Acre Territory, would indicate *H. guianensis* possibly to exist in Peru on the range of hills east of Contamana which center on the Peru-Acre border between 7° and about 8.5° S. However, there is morphological evidence that the type of *H. nigra* is not pure *H. guianensis* but shows some contamination with *H. pauciflora*. The most notable evidence of such contamination appears on the lower leaflet surfaces, where the scales are angular and quite densely crowded. Specimens which match Ducke's *H. guianensis* var. *occidentalis* likewise frequently show this *H. pauciflora* type of lepidote lower leaflet surface. There is a definite tendency for such trees to have considerably weaker rubber than is ordinarily found in true *H. guianensis*. *H. nigra* and what has been known as *H. guianensis* var. *occidentalis* may represent *H. guianensis* with somewhat stabilized admixture of *H. pauciflora* germplasm. A discussion of Peruvian specimens representing hybrids between *H. guianensis* and *H. pauciflora* is given in the succeeding discussion of Putative Hybrids.

1a. HEVEA GUIANENSIS Aubl. var. LUTEA (Spruce ex Benth.) Ducke & Schultes, in Caldasia **3**:249. 1945.

Siphonia lutea Spruce, ex Benth. in Hook. Kew Jour. **6**:370. 1854.
Siphonia brevifolia Spruce, l. c. **7**:194. 1855, nom. nud.
Siphonia apiculata Spruce, ex Baill. in Adansonia **4**:285. 1864.
Hevea lutea (Spruce ex Benth.) Muell.-Arg. in Linnaea **34**:204. 1865.
Hevea peruviana Lechl., ex Benth. & Hook. Gen. Pl. **3**:290. 1880.

[28] The following abbreviations will refer to the condition of the examined collection, *i. e.*: fl. = in flower, fr. = in fruit, st. = sterile.

Hevea lutea var. *cuneata* Huber, in Bol. Mus. Goeldi 3:357. 1902.
Hevea cuneata Huber, l. c. 4:626. 1906.
Hevea brasiliensis var. *cuneata* (Huber) Pax, in Engl. Pflanzenreich 4:123. 1910.
Hevea guianensis var. *cuneata* (Huber) Ducke, in Archiv. Jard. Bot. Rio de Janeiro 6:51. 1933, in part.
Hevea lutea var. *pilosula* Ducke, l. c. 6:53. 1933.
Hevea lutea typica Ducke, l. c. 1933.
Hevea lutea f. *pilosula* Ducke, in Archiv. Inst. Biol. Veg. Rio de Janeiro 2:224, 231. 1935.
Hevea guianensis var. *lutea* f. *peruviana* (Lechl. ex Benth. & Hook.) Ducke, in Inst. Agr. do Norte, Bol. Tec. 10:24. 1946.

In general, as *H. guianensis*, but somewhat larger trees with leaflets erect to somewhat horizontal, tending toward broadly lanceolate and having more distinct pubescence along the midvein. Male buds and calyx lobes slightly but distinctly acuminate; anthers normally 5–7, in two irregular whorls, occasionally with one or more anthers of the lower whorl approaching 1 mm. in length, all other anthers about 0.5 mm. Female buds and calyx lobes somewhat acuminate. Seeds very distinctly quadrangular-kite shaped.

From sterile material alone this variety frequently is hard to distinguish from *H. guianensis*. The floral morphology, which in the two extremes is quite distinct, frequently shows intergrading characters.

Vernacular Names: *jebe debil*, *jebe debil de altura*, *jebe amapa*, *shiringa debil*, *shiringa de altura*, *shiringa de cerro*, *shiringa amarillo* (Peru).

Known Natural Distribution: Upland rain forests of Colombia, Brasil, Bolivia and Peru.

Peru: dept. huanuco: Rio Huallaga: Tingo Maria, upland forest, alt. 675–765 m., fl. Dec. 1942, *Baldwin 2824*, fl. Aug. 1940, *Skutch 4963*, *4966*, old fr. March 1946, *Seibert 2404*, *2406*, *2407*. Rio Pachitea: Pto. Inca, fl. and old fr. Oct. 1945, *Seibert 2184*, old fr., *2185*. dept. san martin: Rio Huallaga: Rio Azul, alt. 800 m., fl. and old fr. July 1945, *Seibert 2087*; Rio Pucarte, st. Aug. 1945, *Langamack s. n.*, old fr. Dec. 1945, *Seibert & Langamack 2261*, *2262*. dept. loreto: Rio Huallaga: Yurimaguas, upland forest, st. Dec. 1942, *Baldwin 2826*, *2827*, fl. Aug.-Sept. 1929, *Killip & Smith 28706*; Rio Paranapura, Chambira Brook, st. May 1943, *Fletcher s. n.*; Rio Shishinagua, st. May 1943, *Fletcher s. n.* Rio Marañon: Pongo de Manseriche, 1923, *La Rue s. n.*; near Borja, fl. Sept. 1940, *Skutch 4080*, st. *4081*, *4082*. Rio Ucayali drainage: Rio Yurac Yacu, Boqueron, alt. 1000 m., old fr. July 1945, *Seibert 2078*; Pampa del Sacramento: Cerro de Chanchahuayo, st. Oct. 1898, *Huber 1377* (type of *H. cuneata* Huber); Rio Yurac Yacu, old fr. July 1943, *Seibert 2074*; Rio Aguaitia, fr. Dec. 1944, *Seibert 1078*, st. Nov. 1945, *Seibert 2234*, fr. *2236*. Rio Ucayali, Requena, st. Jan. 1947, *Carpenter & Lescano s. n.* (P-151 grown from seed at Estación Experimental, Tingo Maria). Rio Amazon: Pinto Cocha, Rio Nanay, st. June 1929, *Lleuelyn Williams 818*; near mouth of Rio Nanay, st. Dec. 1942, *Baldwin 2822*, *2823*; Rio Napo, Singapor, fl. Oct. 1943, *Seibert 1848*, st. *1850*; Rio Ampiyacu, old fr. Feb. 10, 1943, *Russell s. n.*; Huanta, fl. Oct. 1943, *Seibert 1855*, fl. *1856* (intermediate between *H. guianensis* and its variety *lutea*), st. *1857*; Oro Negro, Rio Moto Huayo, old fr. Oct. 1943, *Seibert 1854*. dept. puno: San Gavan, fl. *Collector?* (*H. peruviana* Lechler ex herb.). dept. cuzco: Quince Mil, 1000 m., old fr. May 1946, *Seibert 2426*. dept junin: Satipo, 800 m., old fr. Jan. 1946, *Seibert 2370*, *2371*; fl. Sept. 1940 *Skutch 4974*.

Bolivia: Colonia, Rio Negro, fr. July 1943, *Baldwin 2961*.

Hevea guianensis var. *lutea* is perhaps the most widely distributed entity of the genus. It is a characteristic tree of the Peruvian *montaña*[29]. It is found on

[29] The term *montaña* in Peru refers to all of the heavily forested land east of the Andes. It includes the eastern Andean foothills, as well as the low expanse of the upper Amazonian basin.

much of the Peruvian *tierra altura* and hilly land of the Peruvian Amazon basin, above the flood levels of the Ucayali, Huallaga, Marañon, Napo and the Amazon. It also is found on the eastern Andean foothills, occasionally as high as 5000 feet. As an entity the variety is extremely variable and frequently appears to grade into *H. guianensis*, with which it certainly is most closely allied.

On the basis of floral morphology and pubescence, both on the flowers and lower leaflet surfaces, *H. guianensis* var. *lutea* frequently shows strong tendencies toward *H. Benthamiana*. Morphological evidence might well suggest its having been derived through the hybridization of *H. guianensis* and *H. Benthamiana*, from which was established a true-breeding, relatively stable, but highly variable entity. An occasional plant, although growing far from the known distribution range of *H. Benthamiana*, appears among typical *H. guianensis* var. *lutea* as a probable recombination or throw-back in certain of its aspects to be more referable to *H. Benthamiana*.

In habit and habitat the variety *lutea* is similar to *H. guianensis*, being a rather large tree and, so far as I know, always found on the *tierra altura*. Though frequently seen close to periodically inundated areas, it appears to be confined to the land above inundation level. The position of the leaflets is erect to semi-erect, like that of *H. guianensis* or at most intermediate between that and the horizontal position characteristic of *H. Benthamiana*. Leaflet size and shape, being variable, show a tendency towards an intermediate condition.

The pubescence on the lower leaflet surface is interesting. It will be recalled that in *H. guianensis* there may be slight, sparse whitish pubescence along the midvein, while in *H. Benthamiana* there is typically a rather dense reddish pubescence over the entire lower surface, associated with the veins and veinlets. The indument of *H. guianensis* var. *lutea* is extremely variable. It ranges from sparse whitish to mixed whitish and reddish, or reddish on the midvein and frequently extending to the secondary or branch veins. One case has been found (*Ray Russell s. n.*, May 14, 1943, Santa Rosa, near Pinglo, Rio Marañon, Loreto) where dense whitish pubescence occurs over the entire surface associated with the veinlets.

It appears that this variable pubescence character has at least twice accounted for the description of separate entities, namely, *H. lutea* var. *pilosula* Ducke and *H. Foxii* Huber. Such variations, where *lutea* and *Benthamiana* grow close together, may result from further hybridization between the two entities. In other instances these variations may be natural tendencies toward recombination. The range of variation and distribution as known from specimens at hand appear to be too intergrading for any decisive subspecific naming at the present time.

The presence of a distinct interflush short-shoot is strongly established and allied to that of *H. guianensis*, though here, too, there may on occasion exist a

condition that strongly suggests *H. Benthamiana* influence. The inflorescence habit and the tendency for some leaves of the previous flush to remain until after the appearance of the inflorescence are characteristic of *H. guianensis*, but with modifying influence seemingly suggestive of the *H. Benthamiana* deciduousness. The shape of the male bud and lobe acumination of the flower in anthesis suggest none other than an intermediate condition between *guianensis* and *Benthamiana*. An intermediate condition also is exceptionally well shown in the anthers and in the whorl irregularities. The disk, on the other hand, is strictly that of *H. guianensis*, being represented only by a slight flaring of the staminal column base in the staminate flower. Fruit, carpel thickness and seed shape are those of *H. guianensis*, while seed coloration on occasion appears to show weak *H. Benthamiana* tendencies. Latex flow, quality, and color are highly variable from tree to tree and from region to region. In general, the variety *lutea* produces the weak rubber and relatively poor yield of *H. guianensis*, though individual trees may have relatively high flow, relatively good quality, or frequently a whitish latex; all of which may or may not be due to the probable *H. Benthamiana* background in its phylogenetic history.

Where *H. guianensis* var. *lutea* is found within close proximity to other species it appears that hybridization readily takes place under proper conditions. In Peru, specimens indicate that this variety hybridizes with *H. brasiliensis*, *pauciflora* and *Benthamiana*. Furthermore, evidence of hybridization is not necessarily restricted to the region of close proximity with the other species. Evidence of introgression may be found over considerable distances into the *H. guianensis* var. *lutea* distribution and away from the species with which hybridization must have taken place.

Where *H. guianensis* var. *lutea* comes into the proximity of *H. brasiliensis* in Bolivia, Madre de Dios, and in various places along the Ucayali River, infiltration of *H. brasiliensis* germ-plasm into the *lutea* distribution may be noted from morphological characters. In the Madre de Dios this is perhaps most striking. At Maldonado, *H. guianensis* var. *lutea* comes in from the south and west, stopping rather abruptly at the Rio Madre de Dios. To the north there is at present a gap of some 50 kilometers in which practically no *Hevea* is found. Then suddenly one encounters *H. brasiliensis* from the north and east. It is interesting to note that the *H. guianensis* var. *lutea* from the Maldonado area has considerable infiltration of *H. brasiliensis* germ-plasm, morphologically recognizable. Furthermore, the *H. brasiliensis* germ-plasm appears to have infiltrated some 175 kilometers to the south where a specimen collected by Hodge (*No. 6013*) from the upper Inambari is superficially no different from specimens around Maldonado which show this *H. brasiliensis* introgression. Further to the west, however, as at San Gavan and Quince Mil, one is unable to find morphological indication of *H. brasiliensis* germ-plasm in the specimens of *H. guianensis* var. *lutea*.

The presence of this *H. brasiliensis* germ-plasm is also indicated in the quality of rubber from that area south of the Madre de Dios and east of the Inambari. This area was tapped in the past boom and also during World War II. The rubber is considered as a superior quality *lutea* rubber. Though *H. brasiliensis* itself does not ascend the Rio Pachitea or Rio Pichis, a specimen from Pto. Inca showed strong morphological evidence of its presence within *lutea* and may well account for the superior qualities of weak rubber coming from these areas in general.

From the immediate Iquitos area there are sufficient specimens to indicate strongly the presence of an hybrid swarm on the repeatedly cleared land, some of which is in pasture (pl. 44). Other areas consist of second growth at the present time. From specimens at hand, part of this complex hybrid swarm has resulted from interspecific hybridization of *H. guianensis* var. *lutea* and *pauciflora* in which the majority of the collections show natural segregation to simulate most closely *H. pauciflora*. This appears not to be the entire picture since many other specimens morphologically show segregation of an hybrid swarm between *H. brasiliensis* and *pauciflora*. Here there is likewise a tendency for natural segregation to simulate *H. pauciflora* most closely. Occasionally slight morphological tendencies indicate certain specimens to contain germ-plasm of all three species. However, they are not sufficiently clear-cut or shown in sufficient number of collections to be convincingly measured.

Citation of specimens showing hybridization of *H. guianensis* var. *lutea* with other Peruvian species may be found under the section Putative Hybrids.

2. HEVEA NITIDA Mart. ex Muell.-Arg. in Mart. Fl. Bras. **11**^{2}:301. 1874.

Siphonia nitida Mart. ex Muell.-Arg., l. c., 1874.
Hevea viridis Huber, in Bull. Soc. Bot. France **49**:48. 1902; emend. Huber, in Bol. Mus. (Goeldi) 7:235–236. 1910.

Small to medium-sized tree to 30 m. tall; trunk cylindrical; branches reddish; short-shoots rather conspicuous; bud scales numerous, linear, about 2 mm. long, very early caducous. Leaves partly persistent until after appearance of inflorescence; mature leaflets horizontal to somewhat reclinate, membranaceous but gradually becoming at least subcoriaceous in late maturity, drying reddish, lanceolate to oblanceolate, acuminate, glabrous, concolorous, the scales of the lower surface lacking or so sparse and minute as not to alter its color or lustre, the midvein continuous to the end of the blade tip, not calloused. Flowers whitish-yellow; staminate buds obtuse, becoming somewhat acuminate, not contorted, the short pubescence white, rather uniformly distributed; staminate flowers about 5 mm. long and 3 mm. broad, the calyx lobes slightly acuminate, blunt-tipped, conspicuously calloused, the disk very conspicuous, stellate with 5 acute lobes reaching the lowest anthers, the anthers normally 10, approximating 0.5 mm. in length, in two regular whorls; pistillate buds acute, becoming long-acuminate, not contorted, the pubescence short, white, becoming very sparse towards the lower center of

the lobes and on the tube; pistillate flowers about 9 mm. long and 3.5 mm. broad, the calyx lobes long-acuminate, deeply incised, blunt-tipped, calloused, the disk very conspicuous, of frequently laciniate lobes to 1.5 mm. long, the ovary somewhat glabrescent. Fruit maturing purplish in color, subglobose, emarginate-apiculate, with 3-lobed cross-section; capsules ligneous, explosive, the valves thick, showing little contortion after dehiscence; seeds angular, in cross-section quadrangular kite-shaped toward the micropilar end, becoming hexagonal toward opposite end, to about 21 mm. long and 13 mm. thick. Latex white to buff, not abundant; rubber very inferior.

Vernacular Name: *puca shiringa. shiringa mapa, jebe debil muerto* (Peru).

Known Natural Distribution: Apparently both on rocky hillsides and periodically inundated land but closely associated with old sandstone or granitic outcrops apparently of Cretaceous, Triassic, and Precambrian origin. Colombia, Brasil and Peru.

Peru: dept. loreto: Rio Huallaga: Rio Yanayacu, between Rio Huallaga and Rio Ucayali, swampy land, st. Dec. 1898, *Huber 1534* (type of *H. viridis* Huber). Rio Amazonas: Rio Nanay, Iquitos area, st. June, 1929, *Llewelyn Williams 880.* Rio Putumayo: Occidente on the Peru-Colombia border, fl. 1910, *Fox 2* (type emend. *H. viridis* Huber)—not examined. cultivated material: a living plant brought from the Rio Yanayacu (Peru) by J. Huber, growing at the Jardin Botanico do Museo Goeldi, Belem, Brasil, fl. Sept. 1942, *Archer 7582*, st. Sept. 1931, *Krukoff 1628*, st. Feb. 1924, *La Rue s. n.*

The cultivated specimens cited are of considerable interest since we have so little good material of the species collected from Peru. They appear to represent topotypical cultivated material from Huber's type locality of *H. viridis.* The one flowering collection made by Archer is quite referable to *H. nitida* in floral morphology, the short-shoots and, in general, the leaflets. The lower leaflet surfaces of this and other specimens of the cultivated plant, however, tend to show a minute lepidote condition slightly atypical of *H. nitida.* The scales, notwithstanding, are neither of sufficient size nor density to affect the concolorous aspect. There remains some question, since the leaflets do show a slight *H. brasiliensis* aspect, whether or not Huber's *H. viridis* had some admixture of *H. brasiliensis* germ-plasm.

Having seen only one leaflet from the type of *H. nitida,* Ducke (1935) questioned its affinity with *H. viridis.* Schultes (1945) felt that it should belong with *H. brasiliensis* var. *subconcolor.* Through the excellent photograph, made by the Chicago Natural History Museum, of the entire type specimen of Martius' collection deposited in the Herbarium at Munich, it has been possible to identify *H. nitida* as *H. viridis* with some degree of certainty. The presence of interflush short-shoots, as well as the glossy under-surface of the leaflets, leaves little doubt that *H. viridis* should henceforth be refered to *H. nitida.*

The species appears to be associated with inundable areas along streams but closely associated with, as well as being found on, rocky outcrops or hills of the *catinga*[30] type. *H. nitida* var. *toxicodendroides* (Schultes & Vinton) Schultes is

[30] A light forested, rocky hill is known as a *catinga* in Brasil.

apparently confined to areas of ecological extremes found on the tops of hills jutting out of the Amazon valley floor, in Colombia, as described by Schultes (1944). These hills are flat-topped and may be composed of sandstone, quartzite or granite. They are undoubtedly very old geologically, probably of Cretaceous, Triassic, and in some instances Precambrian age.

Collections of *H. nitida* from Peru are extremely few, and the habitats are not at all well known. Since in Colombia and Brasil the species commonly is associated with the old geologic formations one is incited to look for some indication of similar outcrops in the Peruvian collection areas. Reference to the Geological Society of America's map of South America (1946) indicates such outcrops exist between the Huallaga and the Ucayali, southeast of Yurimaguas. It shows much of the area north of Iquitos, through which the Putumayo passes, to be of Precambrian origin. Although no indication of this is given on Iquitos itself, it must be said that the immediate area on which Iquitos is built is considerably higher than the surrounding country. The soil of this area is not typical of Tertiary deposits of the surrounding lower area, being a yellow, much compacted, clayey sand. It is quite possible that the immediate Iquitos area is itself a relic area. If this is true, the presence of *H. nitida* near Iquitos as represented by the Williams specimen can be satisfactorily explained.

From both Peruvian and extra-Peruvian collections at hand, it appears that *H. nitida* has very widely scattered distributions of rather confined and small areas. This may indicate it to be a survival or relic species. Undoubtedly many more localities of *H. nitida* still exist to be discovered. The same may be said for probable outcrops of these ancient formations jutting out above the Tertiary deposits of the Amazon valley. These probable discoveries will undoubtedly picture more fully the chain of relic areas running southwest from the Guianas and more or less skirting the eastern edge of the northern Andes.

In a number of characters, including floral and fruit structure, habitat association with old geological formations, and the very poor-quality rubber, there would appear to be close relationship of *H. nitida* to *H. pauciflora*. *H. nitida*, however, is easily distinguished by its concolorous leaflets, the exceedingly well-developed staminate disk, and the pronounced acumination of the female bud and mature calyx lobes.

The Peruvian specimens referable to *H. nitida* show no distinct morphological evidence of hybridization with other species. However, it should be stated that the presence of some minute scales on certain specimens could indicate the presence of *H. brasiliensis* germ-plasm. A selection of cultivated *H. brasiliensis*, P-143, from seed collected at Cuipari on the Rio Huallaga and growing at Tingo Maria, on the other hand, shows some floral and lepidote conditions that might indicate slight contamination of *H. nitida*. Unfortunately, the number of specimens is insufficient for making accurate measurements upon which to bear out Baldwin's

suggestion (1947) that *H. brasiliensis* var. *subconcolor* possibly resulted from introgression of *H. nitida* genes into *H. brasiliensis*.

3. Hevea pauciflora (Spruce ex Benth.) Muell.-Arg. in Linnaea **34**:203. 1865.

Siphonia pauciflora Spruce, ex Benth. in Hook. Kew Jour. 6:370. 1854.
Hevea membranacea Muell.-Arg. in Mart. Fl. Bras. 11^2:299. 1874.
Hevea confusa Hemsl. in Hook. Ic. Pl. 6:2, sub *pl. 2570, pl. 2575, figs. 1–3, pl. 2575, figs. 12 & 13*. 1898.
Hevea membranacea var. *leiogyne* Ducke, in Archiv. Jard. Bot. Rio de Janeiro 6:57. 1933.
Hevea pauciflora ssp. *typica* Ducke, in Archiv. Inst. Biol. Veg. Rio de Janeiro 2:239. 1935.
Hevea pauciflora ssp. *coriacea* Ducke, l. c. 1935.
Hevea pauciflora var. *coriacea* Ducke, l. c. 1935.
Hevea membranacea f. *leiogyne* Ducke, l. c. 1935.

Small to large tree to 30 m. tall; branches brownish; trunk cylindrical; short-shoots conspicuous; bud-scales very numerous, deltoid-acuminate, about 3 mm. long, very early caducous. Leaves persistent to partially persistent until after inflorescence maturation and appearance of new flush; mature leaflets horizontal to slightly reclinate, at first membranaceous but slowly becoming quite coriaceous and even revolute in late maturity, usually broadly lanceolate with short obtusely acuminate tip, the pubescence none or of few short, white hairs along part of the midvein, the scales of the lower surface very dense, angular in tile-like compactness, producing a conspicuous whitish surface, the midvein terminating short of the blade tip, calloused or gland-like. Flowers pale yellow; staminate buds obtuse, not contorted, the pubescence white, tomentose, usually dense and rather uniformly distributed; staminate flowers about 3–4 mm. long and 3.5 mm. broad, the calyx lobes acute, blunt-tipped, conspicuously calloused, scarcely acuminate, the disk inconspicuous, but of 5 small gland-like lobes, the anthers normally 10, approximating 0.5 mm. in length, in two regular whorls; pistillate buds obtuse to acutish, not contorted, the pubescence white, conspicuous on the lobes, but scarcely present on the tube and pedicel; pistillate flowers about 5–6 mm. long, 3–4 mm. broad, the calyx lobes acute, blunt-tipped, conspicuously calloused, becoming slightly acuminate, the disk very conspicuous, of acute lobes about 1.5 mm. long, the ovary glabrate to short-pubescent. Fruit maturing purplish red-(or green?) in color, subglobose, emarginate, short-apiculate with 3-lobed cross-section; capsules ligneous, explosive, the valves thick, showing slight contortion at dehiscence; seeds hexagonal in cross-section, quite variable in size, about 13–25 mm. long and 10–18 mm. thick. Latex whitish to tan, oxidizing black; rubber resinous, sticky, very weak and with little elasticity, the yield very poor.

Vernacular Names: No vernacular names referable to this species have been encountered in Peru.

Known Natural Distribution: Apparently associated with geologically old (Precambrian, Triassic, and Cretaceous) outcrops on rocky or sandy slopes, frequently

swampy, in light forest, British Guiana, Venezuela, Brasil, Colombia, and Peru.

PERU: DEPT. LORETO: Iquitos, Estrada Morona, marshy second growth, st. Nov. 1942, *Baldwin 2800*, fr. *2801*, *2802*, fl. *2803*, *2805*, *2806*, fr. *2808*, fl. *2809*, fl. and fr. Dec. 1942, *2815*, *2830*. Vic. Iquitos: wet, grassy area, fl. Oct. 1940, *Skutch 4990*, fl. and fr., *4991*, st. *4992*; Mishuyacu, fl. Sept. 1929, *Killip & Smith 29910*; Punchana, fl. Dec. 1942, *Baldwin 2816*, fl. and fr. *2818*; San Juan, fr., Dec. 1942, *Baldwin 2820*.

Although the above specimens are referred here to *H. pauciflora*, it is questionable whether they represent this species in pure strain. As to their composite morphological characters as a whole, they are taxonomically referable to *H. pauciflora*. In general aspect, certain morphological details of the flowers and seeds, habit, habitat, variable flowering and fruiting time, there are perhaps more than faint indications of germ-plasm infiltrations from *H. brasiliensis* and *H. guianensis* var. *lutea*.

The *H. pauciflora* complex appears to be one of the older entities of the genus. It has a wide range of distribution, but is limited within that range to what appears now to be a belt of small isolated habitats extending from Iquitos in a general northeasterly direction to British Guiana. These habitats become progressively more numerous, somewhat merging into a large area of distribution in southeastern Venezuela and British Guiana. This complex also appears to limit itself to areas which represent geologically old outcrops jutting through the more recent Tertiary Amazon valley deposits. In this distributional respect *H. pauciflora* is similar to *H. nitida* with which it appears closely related morphologically.

The complex has gone through various phases of taxonomic splitting, in which the Guiana material is usually considered as *H. confusa*. The Brasilian material from the Rio Negro and Solimoes is referred to *H. pauciflora* with coriaceous-leaved specimens as *H. pauciflora* var. *coriacea*. Although Hemsley described *H. confusa* as distinct from *H. pauciflora*, he later (1901) came to the conclusion that it was synonymous with the latter. More recently the feeling has been that *H. confusa* is synonymous with *H. pauciflora* var. *coriacea*.

In my comparative morphological studies of material from the entire known range of the complex, it has become apparent that the differences in leaflet texture is not inherent, but a condition due to maturity. Unlike most other species (possible exceptions are *H. nitida* and *H. rigidifolia*), the leaflets of *H. pauciflora* appear to take a relatively long time to reach their full texture maturity. Although the leaflets reach mature size very shortly after their appearance, they are at first quite membranaceous and for several months gradually become coriaceous. This species tends to hold its leaves until after the appearance of the new flush and the new leaves have reached mature size. Through actual specimens, it has been possible to see the previous year's coriaceous, revolute leaflets, and at the same time see the current year's mature, membranaceous leaflets. This leads me to believe that no valid varietal difference can be made on the basis of leaflet texture. A search has been made, with little success, to find other morphological characters sufficiently stable to base taxonomic segregation of these supposed entities. The specimens at

hand show some striking variations in fruit and seed size, though perhaps no greater than is the range in *H. brasiliensis*. The seed shape would appear, however, to be of a rather uniform pattern, having an hexagonal cross-section. There are so few specimens of the *pauciflora* complex having seed that I am unable to determine whether or not the seed differences are of varietal or subspecific value.

Spruce (Bentham, 1854) has mentioned that the seeds of *Hevea* on the Rio Negro are prepared and eaten by the Indians; and Dr. Baldwin informs me that *H. pauciflora* is frequently grown by the Indians in their yards for the seeds which they eat (Baldwin, 1947). It could be possible that in the hundreds of years Indians have been along the Rio Negro, they have not only distributed the species outside of its natural habitats, but also subconsciously selected for seed size. Perhaps some of the exceptionally large-seeded specimens are coming from old planted trees.

A further character which may or may not be of taxonomic use in the complex lies in the color of the maturing fruit pod. Apparently it usually matures purplish red, but sometimes the color appears to be green. Until further evidence can be shown that valid morphological differences of taxonomic significance exist within the complex, it seems best to consider the complex as one entity under *H. pauciflora*. It is recognized that there appear to be few genetic boundaries to prevent natural hybridization with other species when natural or man-made conditions are favorable for it. This may be an important factor in the seeming confusion within the *H. pauciflora* complex.

Both *H. humilior* and *H. paludosa* have been described from the immediate vicinity of Iquitos. The type material, in both species, is thought to represent segregating material from an hybrid swarm derived through interspecific hybridization of *H. pauciflora* and *H. guianensis* var. *lutea*. In both *H. paludosa* and *H. humilior* the material most closely simulates *H. pauciflora*, and recent collections have been labeled *H. pauciflora* var. *coriacea* by Ducke. The presence of *H. guianensis* var. *lutea* is morphologically more difficult to distinguish in the types of *H. humilior* than in *H. paludosa;* but, at least through bud acumination and pubescence characters, there can be little doubt of its presence.

If *H. pauciflora* and *H. guianensis* var. *lutea* were the only species concerned in producing the Iquitos hybrid swarm the problem would be relatively simple. The swarm is complicated in that segregates of *H. pauciflora* × *brasiliensis* also appear. Morphological evidence from the leaves, short-shoots, bud acumination and contortion, calyx-lobe acumination, and seed characters can leave little doubt of such a condition existing.

Although specimens show natural segregation most closely towards forms of the *H. pauciflora* parent, there is evidence from cultivated trees planted at Hac. Chanticlair that, given ideal and uniform growing conditions, gradation takes place in the direction of both parents. A discussion of this will be found under

H. brasiliensis × *pauciflora* in the section Putative Hybrids. The Iquitos hybrid swarm complex is still insufficiently known and collected to give more than faint, inconclusive evidence that certain specimens show influence of all three species within the same plant. Undoubtedly future collections will show this to occur. Discussion and citation of specimens from the Iquitos hybrid swarms may be found under the section Putative Hybrids.

It seems significant that frequently the same tree is both in fruit and flower at the same time. This is borne out by the range of flowering dates when grouping together all specimens from Iquitos cited as *H. pauciflora, H. guianensis* var. *lutea* × *pauciflora,* and *H. brasiliensis* × *pauciflora.* Flowering appears to occur between July and March; furthermore, it must frequently occur twice a year to account for flowers and mature fruit on the same tree. Segregation along morphological lines not only is taking place, but it appears that the normal flowering time regulator has been upset, or at least modified to fit in with the extremely variable, seasonal conditions from year to year and within the year found around Iquitos. Frequent definite wet and dry periods alternate throughout the year. This could give rise to a set of conditions which, when correlated and emphasized by such man-made conditions as deforestation of the jungle, with resultant grazing and second-growth, could well fit in with the unstable pattern of both frequent and sporadic flowering.

The large-scale man-made changes in the immediate area of Iquitos (pl. 44), and the natural conditions within that area, in which all three parent species exist, together with the few genetic boundaries, would all seem to constitute an ideal set of conditions for the development of such hybrid swarms. Since most of the members of the swarms appear most closely to simulate *H. pauciflora,* it must be assumed that the man-made changes have simulated most closely the habitat of that species.

The immediate area around Iquitos is somewhat higher in elevation than the surrounding country, and the rather compacted, sandy, clay soil is not typical of the surrounding lower areas. It appears that Iquitos might well represent an isolated Triassic or Cretaceous sedimentary outcrop, especially since we do find *H. pauciflora,* a species which in other regions seems to be confined to such old outcrops. Practically all of this Iquitos area has been cut over in the past, not only once but perhaps many times. It was presumably inhabited by Indians long before the coming of white man. Here, then, rises the question suggested immediately following the citation of the specimens under *H. pauciflora:* are these specimens pure strain *H. pauciflora?* It might be possible that *H. pauciflora* in pure strain at Iquitos long since has been destroyed by man, but still persists in the form of an hybrid swarm which is attempting to maintain its identity as *H. pauciflora.*

Even though *H. pauciflora* were not originally indigenous to Iquitos, we know that the seeds of this species were eaten by the Indians of the Rio Negro and that they transported seeds for planting in their yards. It would not be too hard to presume that *H. pauciflora* may have been introduced into Iquitos before white man arrived. Successive introductions of this species along the rivers at various points would have led to a man-induced, natural selection for adaptation to a wide range of habitats.

Food for man is scarce in the Amazonian jungle and the Indian augments his jungle harvests with planted root and seed crops, not only in his garden but frequently at scattered points along his hunting trails. One evidence of this is the presence of several Brasil-nut trees, *Bertholletia excelsa,* near the river between Iquitos and its suburb, Punchana. The Brasil-nut tree apparently is not indigenous as far up the Amazon as Iquitos. Its size, as well as the opinion of the older inhabitants, indicates it to have been planted by Indians long before Iquitos was a modern town. The "peach palm," *pijuayo* or *pifuayo, Guilielma sp.,* a native of the Andean slopes, is found frequently in isolated stands of a few trees on well-drained, ideal camping spots near waterways, apparently all through the Amazon valley. These instances are able further to substantiate a theory that *H. pauciflora,* too, may have been introduced by the Indians.

4. Hevea Benthamiana Muell.-Arg. in Linnaea **34**:204. 1865.

Small to medium-sized tree to 25 m. tall; trunk conspicuously swollen toward base; branches reddish gray; short-shoots inconspicuous, of narrow ring of bud-scale scars; bud scales few, thin, linear-acuminate, about 3 mm. long, very early caducous. Leaves deciduous before the appearance of the inflorescence; mature leaflets horizontal to slightly reclinate, firmly membranaceous, very broadly lanceolate to oblanceolate, shortly acuminate, drying reddish, usually reddish-pubescent below, the scales of the lower surface rather dense, whitish, more or less lens-shaped in outline, the pubescence usually dense, typically reddish over the entire surface, and confined to the veins and veinlets, the midvein continuous to the blade tip, not calloused. Flowers yellowish; staminate buds acuminate, not contorted, uniformly dense, long and reddish-pubescent, the pubescence longer and more dense at the point of abscission; staminate flowers about 3–4 mm. long and 2 mm. broad, the calyx lobes acuminate, not contorted and not callose-tipped, the disk of 5 small but conspicuous lobes, the anthers normally 8–10, about 0.5 mm. long, in two irregular to regular whorls; pistillate buds acuminate, not contorted, densely reddish and longish-pubescent, the pubescence becoming less dense towards the base of the tube; pistillate flowers about 6 mm. long and 2.5 mm. broad, the calyx lobes acuminate, not contorted and not callose-tipped, the disk inconspicuous, of very short lobes, the ovary densely short-pubescent. Fruit maturing green, subglobose, emarginate-apiculate, with 3-lobed cross-section; capsules ligneous, explosively dehiscent, the valves rather thin, not noticeably contorting at dehiscence; seeds ellipsoidal in cross-section, ventrally compressed,

but otherwise rounded with scarcely any indication of angling, about 19 mm. long and 14 mm. thick, the brilliant, clear, brownish mottling having a whitish background. Latex white, abundant, the rubber and yield considered second only to that of *H. brasiliensis*.

VERNACULAR NAMES: Thus far, no vernacular names have been encountered in Peru.

KNOWN NATURAL DISTRIBUTION: Apparently confined to the deeply inundated areas and *igapos*[31] near the major streams along and north of the Amazon, southern Venezuela, Colombia, Brasil, and apparently along the lower Peruvian portion of the Rio Putumayo.

Of this species, I have seen no material of apparent pure strain collected from Peruvian soil. Schultes (1945) states that *H. Benthamiana* occurs along the Rio Putumayo of Colombia below Arica, so it is quite possible it may exist on the Peruvian side as well. I have seen specimens, apparently representing hybridized forms of *H. guianensis* var. *lutea* × *Benthamiana*, from the Peruvian-Colombian Putumayo, which have been referred to *H. Foxii* and *H. glabrescens*. These are discussed under the section Putative Hybrids.

Since no specimens from Peru yet coming to my attention apparently have represented pure strain *H. Benthamiana* I am at present giving no synonymy for the species. However, it has been necessary to revise the descriptive terms for the species in keeping with the morphological revisions of the other Peruvian species. This has been done largely from an isotype specimen of *H. Benthamiana, Spruce 2560*, a very fine specimen collected from the Rio Negro region of Brasil, near Panure on the Rio Vaupes.

Many varieties and forms of *H. Benthamiana* have been described, and it appears that most of them have conspicuous short-shoots, a character which is not conspicuously present in typical *Benthamiana* material. Ducke (1943), Schultes (1945) and Baldwin (1947) recognize that *H. Benthamiana* hybridizes rather readily with the *H. guianensis* complex, *H. pauciflora* and *H. Spruceana*. Examination has shown that many specimens considered as varieties of *H. Benthamiana* simulate it in general, except for having the conspicuous short-shoots. This, as well as the presence of other morphological characters, has convinced me that many of these named varieties are actually the result of very frequent hybridization between *H. Benthamiana* and these other species.

5. HEVEA BRASILIENSIS (HBK.) Muell.-Arg. in Linnaea **34**:204. 1865.

Siphonia brasiliensis Willd., ex Juss. Euphorb. Gen. 40, 113, *pl. 12, fig. 38b*. 1824, nom. nud.
Siphonia brasiliensis HBK. Nov. Gen. et Sp. 7:171. 1825.
?*Siphonia Kunthiana* Baill. Etud. Gen. Euphorb. 326. 1858.
Hevea janeirensis Muell.-Arg. in Mart. Fl. Bras. 11^2:706. 1874.
Hevea Sieberi Warb. Kautschukf. 32–33, *fig.* 1900.
?*Hevea Kunthiana* (Baill.) Huber, in Bol. Mus. Goeldi **3**:349. 1902.
Hevea brasiliensis var. *angustifolia* Ule, in Tropenpflanzer, Beiheft **6**:8. 1905.
Hevea brasiliensis var. *latifolia* Ule, l. c. 1905.
Hevea brasiliensis var. *stylosa* Huber, in Bol. Mus. Goeldi **4**:640. 1906.
Hevea Randiana Huber, l. c. 636. 1906.

[31] *Igapo* is a Brasilian word for areas subject to very heavy yearly inundation and which are rather permanently swampy.

Hevea brasiliensis var. *Randiana* (Huber) Pax, in Pflanzenreich 4:123. 1910.
Hevea brasiliensis var. *janeirensis* (Muell.-Arg.) Pax, l. c. 121. 1910.
Hevea brasiliensis var. *acreana* Ule, in Engl. Bot. Jahrb. 50:14. 1914.
Hevea brasiliensis f. *typica* Ducke, in Arch. Jard. Bot. Rio de Janeiro 6:55. 1933.
Hevea brasiliensis var. *subconcolor* Ducke, l. c. 1933.
Hevea brasiliensis f. *subconcolor* Ducke, in Archiv. Inst. Biol. Veg. Rio de Janeiro 2:224. 1935.
Hevea brasiliensis f. *Randiana* (Huber) Ducke l. c. 1935.
Siphonia ridleyana Cook, in Jour. Wash. Acad. Sci. 31:46. 1941.

Large tree to 50 m. tall; branches grayish brown; trunk cylindrical, but noticeably swollen towards base when growing in periodically inundated land; short-shoots inconspicuous, of narrow ring of bud-scale scars; bud scales few to about 10, linear-deltoid, about 3–4 mm. long, early-caducous. Leaves deciduous before appearance of inflorescence; mature leaflets reclinate, membranaceous, usually lanceolate to broadly lanceolate with rather long-acuminate tip, glabrous, the scales of the lower surface whitish and roundish in outline, the midvein continuous to end of blade tip or extending slightly beyond, not calloused. Flowers creamish yellow; staminate buds noticeably acuminate, slightly contorted, the pubescence short, white, uniformly distributed; staminate flowers about 5 mm. long and 2.5 mm. broad, the calyx lobes acuminate, blunt-tipped, calloused, and contorted, the disk inconspicuous, of 5 rudimentary lobes or swellings, the anthers 10, approximating 0.5 mm. in length, in two regular whorls; pistillate buds noticeably acuminate, slightly contorted, the short pubescence white, becoming sparsely distributed below the lobes on the tube; pistillate flowers about 7 mm. long and 3 mm. broad, the calyx lobes long-acuminate, blunt-tipped, calloused and contorted, the disk inconspicuous, the ovary silky-pubescent. Fruit maturing green in color, subglobose, emarginate-apiculate, with 3-lobed cross-section; capsules ligneous, explosive, the valves thick, showing no contortion at dehiscence; seeds ellipsoidal in outline, ventrally compressed but usually without noticeable angling in the ventrally compressed ellipsoidal cross-section, variable in size, 16–38 mm. long, 14–24 mm. thick. Latex white or rarely cream to yellowish; rubber and yield superior for the genus.

VERNACULAR NAMES: *jebe fino, shiringa fino, shiringa legitimo, shiringa* or *seringa* (Peru), and *seringueira* (near the Peru-Brasil border).

KNOWN NATURAL DISTRIBUTION: Periodically inundated land along the Amazon and the lower courses of its larger tributaries in Venezuela, Colombia, Brasil and Peru. Also on well-drained inter-river plateaus or gently rolling land in Parana, southeastern Amazonas, Acre and northern Matto Grosso, Brasil; Pando, Beni and northern La Paz, Bolivia; and Madre de Dios, Peru.

PERU: DEPT. SAN MARTIN: Rio Huallaga above Yurimaguas, periodically inundated land along Rio Cuipari (seed grown at Estación Experimental Agrícola de Tingo Maria), fl. Aug. 21, 1946, *Carpenter & Lescano s. n.* (P-142), fl. Sept. 1946, *Carpenter & Lescano s. n.* (P-143), fl. Aug. 1945, *Seibert 2273*. DEPT. LORETO: periodically inundated land: Rio Marañon, confluence with Rio Ucayali, st. Dec. 1942, *Baldwin 2828*. Rio Pacaya, affluent of Rio Ucayali, st. Mar. 1943, *Russell s. n.* Rio Tapiche, affluent of Rio Ucayali, Uscar, st. Nov. 1943, *Seibert 1893;* Callao, st. Mar. 3, 1943, *Russell s. n.*, st. Mar. 4, 1943, *Russell s. n.* Rio Ucayali, Lago Curuhuaiti, above Requena, st. Nov. 1943, *Seibert*

1882, 1883, 1884. Rio Amazon: Rio Itaya, st. May 1929, *Llewelyn Williams 206;* Iquitos: Punchana, st. Dec. 1942, *Baldwin 2821,* Pró, fl. Aug. 1929, *Llewelyn Williams 2003;* Yana Mono Island, mouth of Rio Napo, st. Oct. 1943, *Seibert 1877;* Oran, below mouth of Rio Napo, st. Oct. 1943, *Seibert 1853;* Firmeza, across from Pebas, old fr. Oct. 1943, *Seibert 1861;* Quebrada Yanayacillo, st. Oct. 1943, *Seibert 1864,* fl. *1876;* Fortaleza, Rio Peruate, fl. Oct. 1943, *Seibert 1872, 1873,* st. *1874;* La Victoria, fl. Aug.-Sept. 1929, *Llewelyn Williams 2931;* Caballo Cocha, st. Aug. 1929, *Llewelyn Williams 2176;* (From Caballo Cocha seed progeny grown at Tingo Maria) fl. Aug. 1945, *Seibert 2275, 2277,* fl. Aug. 1946, *Carpenter & Lescano s. n.* (P-146), fl. Sept. 1946, *s. n.* (P-146), fl. Aug. 1946, *s. n.* (P-147); Islandia, mouth of Rio Yavari, fl. and fr. Oct. 1940, *Skutch 4087;* Rio Ataquari, Peru-Colombia border, st. Oct. 1943, *Seibert 1869.* DEPT. MADRE DE DIOS: Usually on well-drained land between streams, soil yellowish to reddish, sandy, clay loam: Rio Acre drainage: Iñapari, Centro Viejo, st. June 1945, *Seibert 2053.* Rio Tahuamanu drainage: Iberia: fl. July 1944, *Seibert 1939;* Centro Alianza, st. July 1944, *Seibert 1932;* Centro Arrozal, st. May 1945, *Seibert 2021,* st. June 1945, *2023, 2024, 2025, 2026,* old fr. *2027, 2028, 2030, 2031,* st. *2032,* old fr. *2033;* Centro Brussellas, st. July 1944, *Seibert 1935, 1936, 1937, 1938;* Centro Miraflores, st. Apr. 1944, *Seibert 1904,* old fr. *1905,* st. July 1944, *Seibert 1933, 1934,* fl. Aug. 1945, *Seibert 2130,* fl. and old fr. *2141, 2142, 2143, 2144;* Centro Portillo, fl. Oct. 1944, *Seibert 1955,* st. *1956,* fl. *1957, 1958, 1959, 1960, 1961, 1962, 1963,* st. *1964, 1965;* Centro Primavera, st. June 1945, *Seibert 2060,* old fr. *2062, 2065;* Centro Urquilla, st. June 1944, *Seibert 1925;* Centro Villa Nueva, st. June 1944, *Seibert 1926.*

BOLIVIA: DEPT. PANDO: On well-drained land between streams, soil yellowish loam to sand-clay loam: Rio Acre drainage: Cobija, st. Dec. 18, 1923, *La Rue s. n.* (three collections); "one hour east" of Nazaret, fl. Aug. 1945, *Seibert 2115;* Nazaret to Nauruediño, between Acre and Tahuamanu drainage, fl. and old fr. Aug. 1945, *Seibert 2116;* Ultimatum to Peru border, Rio Tahuamanu drainage, fl. and old fr. Aug. 1945, *Seibert 2120.* Rio Tahuamanu drainage: Porvenir, st. Dec. 23, 1923, *La Rue s. n.* Rio Abuna drainage: Rio Pacahuaris, Santo Domingo, old fr. June 1943, *Baldwin 2955, 2957.* DEPT. BENI: well-drained *tierra altura:* Riberalta: fl. Sept. 28, 1923, *Wier s. n.;* Hac. El Prado, fl. Aug. 1945, *Seibert 2102;* junction of Beni and Madre de Dios rivers, fl. Aug. 1886, *Rusby 885,* Ivon, Rio Ivon, st. Feb. 1922, *White 2378.* Rio Guapore drainage: Lago Guachi, fl. Sept. 1943, *Baldwin 2998.*

Within the Department of Loreto, along the Amazon (upper Solimoes) and its larger tributaries, as the lower Huallaga, Marañon and Ucayali, *H. brasiliensis* is almost uniformly associated with the periodically inundated areas. Very exceptionally, it is associated with the slightly higher, non-inundable land adjoining the periodically flooded areas, though the distance and the altitude between the two habitats may be but a few meters.

As to the origin of *H. brasiliensis* as a species, I hesitate at this time to draw any definite conclusions. Morphologically, it appears to be a complex made up of characters both simulating and distinct from other species. Its leaflets are more reclinate than in any other species except possibly *H. rigidifolia,* which, however, are not very well known from this standpoint. The short-shoots of *H. brasiliensis* are less pronounced than in any other species. Typically it lacks any pubescence on the lower mature leaflet surfaces. The staminate and pistillate calyx lobes are interesting in that they show small calloused tips. Calloused lobe tips are found in no other species except *H. pauciflora* and *H. nitida,* where they are quite pronounced. The calyx lobe tips of *H. brasiliensis* show some variation, but, in general, are less conspicuous, suggesting an intermediate condition between callosity and

the normal acute tip. Both the disk and number of anthers (10, in two regular whorls) appear to be quite constant. The fruit, the valves, and, in a way, the seeds perhaps most closely resemble those of *H. pauciflora*. The lower leaflet surface is strikingly similar to that of *H. microphylla*. As a species, *H. brasiliensis* forms the largest trees in the genus. Its most outstanding feature is its superior latex yield and rubber quality.

In contrast to the preferred habitat of *H. brasiliensis* along the Amazon, its habitat in the northeastern portion of the Department of Madre de Dios and the adjoining regions of Brasil (Acre) and Bolivia consists of well-drained, rolling land. The soil here is a friable, reddish to yellowish, sandy, clay loam of excellent quality. Although very little of this area, even along the major streams, is subject to long-period flooding, the species is not at all common where considerable flooding occurs.

Although throughout much of its range *H. brasiliensis* is associated with periodically inundated conditions, such is not the case in its southwesternmost limits of distribution. Usually it is not found on inundable land in Bolivia, Matto Grosso or in the state of Parana. *H. brasiliensis* of the Tapajos and regions between the Tapajos and the Xingu apparently is found on the well-drained plateau areas above the rivers. Due to lack of sufficient collections it is not clear to me where, or if, there is a distinct zone of transition between upland and lowland *H. brasiliensis*. The critical area for such determination will lie within the southern half of the Brasilian State of Amazonas. Men in Peru who have been in the upper Yavari, the Rio Blanco, and the Rio Maquia, all rivers which have their source from the range of hills along the Peruvian border adjoining northwestern Acre Territory, have reported that *Hevea brasiliensis* gradually takes to the higher, well-drained land.

There are several interesting cases, from both the Peruvian and Bolivian border areas, in which specimens referable to *H. brasiliensis* show various gradations of *H. guianensis* var. *lutea* influence in their characters, and vice versa. As will be discussed under Putative Hybrids between these two entities, there is evidence that the *tierra altura H. brasiliensis* is a geographic race resulting from introgression and ecotypic selection and carries a slight contamination of *H. guianensis* var. *lutea* germ-plasm.

In southern Madre de Dios and the adjoining region of Puno of Peru, and in the Departments of La Paz and Beni of Bolivia, both the limits of *H. brasiliensis* entering from the northeast and *H. guianensis* var. *lutea* descending along the Andean foothills are quite sharp and distinct, a comparatively narrow belt existing between the two (seemingly of varying width) in which very little *Hevea* is found. Typified by the area between Maldonado and the Rio Manuripe in Madre de Dios, and between Rurrenabaque and Mapiri in Bolivia, it is along the border areas of *H. guianensis* var. *lutea* that there appears to be further hybridization between the two entities. This has resulted in a zone of intergradation along the

zone of intergrading habitat between the relatively flat, rolling area of *tierra altura H. brasiliensis* and the steep foothill slopes of *H. guianensis* var. *lutea.*

Hybridization between the *tierra baja H. brasiliensis* and *H. guianensis* var. *lutea* is indicated in the following specimens: from *tierra altura* areas on the Rio Pachitea; near the junction of the Marañon and Ucayali, at Nauta; on the lower Napo; and at the mouth of the Yavari. The fact that specimens are found which are intermediate or approach one or the other of the species indicates that natural hybridization occurs between the two entities at any place where conditions are such that the two species come close together. There may be a resulting tendency for simultaneous and parallel development of the upland race of *H. brasiliensis* at many places throughout the Amazon valley.

Citation of hybrid specimens and further discussion may be found under the section Putative Hybrids, where reference likewise is made to interspecific hybridization involving *H. pauciflora.*

Natural Occurrence and Species Range

The accompanying map shows the distribution of the *Hevea* species in Peru and bordering areas of neighboring countries. Collections and collecting stations of *Hevea* in Peru are far too few upon which to base a complete and accurate distribution map. Little is known of large areas between many collecting stations cited with the species descriptions. It has been necessary to fill in a large proportion of the map with questionable data gained from hearsay, transient rubber tappers, reports of rubber coming from various isolated areas, and from impressions gained through having flown over much of the lowland area of Peru east of the Andes.

Ule (1905) has presented a map showing the region of the entire Amazon valley in which species of *Hevea* are found. It presents a rather good picture of the distribution of *H. brasiliensis* and part of *H. discolor* sensu *H. Benthamiana,* but makes no attempt to show distributions of other species. The picture presented for Peru is very sketchy and incomplete. The map given in Schurz *et al.* (1925), also showing the entire Amazon valley, is not much more complete in that it deals only with *H. brasiliensis* and *H. Benthamiana.* The distribution of *H. Benthamiana* on the Peruvian Amazon and Napo appears to be entirely inaccurate. *H. brasiliensis* distribution in Peru is shown to extend into regions known to have *H. guianensis* var. *lutea,* a very abundant species in that country but not shown on the map. Neither map gives the over-all picture of *Hevea* species distribution in Peru.

It appears that the genus reaches its southernmost distribution of about 16° S. in the Department of La Paz, Bolivia, and its westernmost limits around the Pongo de Manseriche in the vicinity of the Rio Marañon in the Department of Amazonas, Peru. In both these extremes the genus is represented by *H. guianensis* var. *lutea,* as it is for the altitudinal extremes of the genus where it occasionally reaches 5000

feet on the Andean foothills.

Specific distributional features have been discussed under each species, but little has been said concerning plant associations found with the Peruvian *Hevea* species. In many cases these features are not sufficiently known for present discussion. In northwestern Madre de Dios, where Peru joins Brasil and Bolivia, it is significant that *H. brasiliensis* is associated with the Brasil-nut tree, *Bertholletia* cf. *excelsa,* which in this region has somewhat smaller fruit and apparently better-flavored kernels than trees from lower on the Amazon. Here both trees prefer and are usually confined to the well-drained *tierra altura.* Up to as many as eight trees per hectare of *H. brasiliensis,* and slightly less of *Bertholletia,* have been found on average areas of more dense distribution. Neither *Hevea* nor *Bertholletia* is uniformly distributed throughout the entire area. Both appear to be in local "pockets" of from about 10 to 100 sq. kilometers, separated by several kilometers in which the distribution of *Hevea* especially may be quite sparse. These localized areas of dense *Hevea* distribution are known in that region as *centros;* these being subdivided into *colocasiones* in which several *shiringeros* or rubber tappers live more or less together, working their individual *estradas.*

As a whole, the area could be classed as a *Hevea-Bertholletia* forest in which these two species are most frequently encountered and form the largest of the forest giants. This area of Madre de Dios and that adjoining in Bolivia are frequently characterized by having a thick undergrowth of semi-climbing spiny bamboo, *paca, Guadua tomentosa* Hack & Lindn.[32] *(Seibert 2068).* These mats of *Guadua* undergrowth, *pacales*[33], are frequently many square kilometers in extent in which little other tree growth than *H. brasiliensis* and *Bertholletia* may be found. It appears that the *Guadua* is slowly enveloping the forest, replacing the old trees as they die out and preventing any other trees from gaining a foothold. It is perhaps because both *Hevea* and *Bertholletia* form such old trees that they still persist in these *pacales.* Many *estradas* are at least partially located in these bamboo areas, in which trail maintenance is a difficult and time-consuming task because of the rapid growth and viciously spiny nature of the undergrowth. Ule (1914) has mentioned this bamboo association with *H. brasiliensis* considerably further to the northeast in Brasil, referring it to *Guadua Weberbauri* Pilger.

Unlike the *Hevea brasiliensis* of the Madre de Dios, that of the Amazon and lower Ucayali grows in the periodically inundated land adjoining the rivers where *Bertholletia* is non-existent and *Guadua* is seldom found. The distribution of *H. brasiliensis* in Peru and adjoining Brasil and Bolivia is apparently not too dissimilar to that shown by Record & Hess (1943) for *Swietenia macrophylla,* Coaba, the Peruvian mahogany. Although *Swietenia macrophylla* extends into regions where *H. guianensis* var. *lutea* is found, in the Iquitos area it occurs on the periodically inundated areas skirting the river with *H. brasiliensis,*

[32] Provisionally determined by Dr. F. A. McClure.
[33] *Pacales* are areas in which the dominant vegetation is *paca, Guadua* sp.

HEVEA DISTRIBUTION IN PERU

100 0 100 200 300 400 500

KILOMETERS

- *H brasiliensis*
- *H. guianensis*
- *H. " var. lutea*
- *H. pauciflora*
- *H. nitida*
- *H Benthamiana*

DISTRIBUTION OF SPECIES OF *HEVEA* IN THE REPUBLIC OF PERU AND BORDER REGIONS OF ADJOINING COUNTRIES

Base map copied from the Map of the Americas, South America—sheet North, 1:5,000,000, American Geographical Society of New York, 1942. 5/6 original size.

but appears to make its best growth on the *tierra altura.* In the Madre de Dios area it is found with *H. brasiliensis.*

Cedrela odorata in Peru includes in its hillside forest form *cedro virgin,* growing in areas which are typical for *H. guianensis* var. *lutea,* while its *tierra baja* form, found on periodically inundated land in the Iquitos area, is frequently associated with *H. brasiliensis.*

It is not known to what extent the distribution of *H. guianensis* overlaps that of *H. guianensis* var. *lutea* in Peru and adjoining areas. Specimens which are referable to *H. guianensis* appear to exist along with those of *H. guianensis* var. *lutea* in a number of regions. On account of the sparsity of good *H. guianensis* material, no accurate lead can be given as to whether or not the two entities are separated ecologically. It appears that the areas where *H. guianensis* is recognizable taxonomically also contain recognizable hybrids between either *H. guianensis* and *pauciflora* or *H. guianensis* var. *lutea* and *pauciflora.* The distribution of *H. guianensis* as represented on the map is of that which Ducke interprets as *H. guianensis* var. *occidentalis.* This variety has been suggested in the section, Putative Hybrids, as being of introgressive origin. Its distribution might suggest for the most part, that, though in morphological aspect it is referable to *H. guianensis* in that there is a predominance of 5 large anthers in one irregular whorl, it might even have resulted from *H. guianensis* var. *lutea* × *H. pauciflora.* The conflicting evidence at hand strongly suggests that these areas of overlapping distribution are badly in need of further collection and field study.

This type of distribution mapping, though probably inaccurate in many respects, serves as a much-needed guide in pointing out areas badly in need of further field study and collection. It should be noted that the distribution areas showing *H. nitida* and *H. pauciflora* also are points at which further field study is much needed. Although not plotted on the map, R. de Lemmos Froes recently found *H. Spruceana* to extend up the Amazon to the Rio Jutai, above Fonte Boa. It is very doubtful, however, that this species will ever be found to occur in Peru in pure strain.

Historical Ecology

In considering the origin and distribution of *Hevea* it will be necessary to have a clear picture of the geological history of the Amazon valley and its surroundings. Though many details are lacking, the Geological Society map for South America (1946) gives the compiled knowledge from existing published works on the subject.

The Andean uplift, which skirts the western reaches of the Amazon valley, peters out to the north and west of the Orinoco River in Venezuela. Previous to the late Mezozoic folding of the Andes, or at least previous to their Pliocene uplift, it is thought that much of the drainage of the present Amazonian region passed towards the Pacific. At that time, it would appear that an older range, still very

prominent in the Guianas (Maguire, 1945) and typified by Cerro Duida (Tate & Hitchcock, 1930) and Mt. Roraima (Tate, 1930) in Venezuela and British Guiana, extended towards the southwest as well as southeastward through the lower, present Amazon region. This range, presumably, was continuous with the ranges still extant which skirt the southeastern reaches of the Amazon valley in Goyaz and Matto Grosso.

The Andean uplift must have stopped the westward flow of water to the Pacific, resulting in a huge, inland lake now evidenced by the Tertiary deposits of the Central Amazonian basin. This lake, in an effort to find an outlet, had to push through the ancient, eastern range. Its rising waters at the same time isolated many higher areas as islands within it. As evidenced by the extremely low divide existing between the Amazon and Orinoco drainage at an actual junction of the upper Casiquiare and the Orinoco in Venezuela, the Amazonian lake may possibly have broken through northward to the Atlantic previous to its present course. Further study of existing maps might indicate that a break once existed at the present low divide between the upper Guapore and Paraguay rivers, flowing out southward through the Parana basin also previous to its final breakthrough and the formation of its present course toward the east.

In light of such complicated geological history as major changes in water-flow to the four directions (referred to as "sloshing" by Baldwin, 1947) and the presence of a huge inland lake in which isolated peaks of an old land mass existed without being flooded, one can begin to picture the genus as having had a complicated genetic history in its adaptation to major ecological changes. Presumably, the genus had its origin on the Triassic land mass or even old Precambrian outcrops at that time and subsequently exposed permanently. If we can base any faith on the presumption that the primitive types of the genus still exist associated with these old formations, we must consider *H. guianensis* and *H. pauciflora* as being those types. From these, and possibly through intergeneric hybridization in some cases with *Cunuria* or other closely allied genera (Baldwin, 1947; Baldwin and Schultes, 1947), other species were derived and ecotypically selected. Such natural selections were for adaptation to a succession of changing water-flow directions, new habitats caused by the draining of the huge lake, and development of the present Amazon drainage system.

Presumably the genus had been evolved previously and was encroaching on the newly formed land as the lake subsided. It is possible that, due to lake conditions and flood waters, seed dispersal at the time could have been in all directions and very widespread through water currents to many portions of the subsiding lake shores. It probably would have been necessary for the genus to evolve types which were adapted to very wet and more or less permanently inundated conditions. Such types are still extant in the form of *H. Spruceana, Benthamiana* and *microphylla*, as are types which prefer only periodical inundations as *H. brasiliensis* and *nitida*. Such adaptations have been evolved not only through interspecific

hybridization, chromosome aberrations, and natrual selection, but also possibly through intergeneric hybridization. This may be substantiated by *H. Spruceana* which suggests strong *Cunuria* influence in the structure of its fruit and in habitat preference.

As the lake subsided, leaving the shores high and no longer subject to inundation except along the forming stream channels, there was further need for the evolution of types which could again persist on well-drained land. This habitat was to typify the greater part of the Amazon valley. In the light of this, we find at present that *H. guianensis* var. *lutea* fits into such a habitat pattern and has the largest distribution of any of the species. Also, we find that *H. brasiliensis* has a rather large distribution south and west of the Amazon. It exists not only as a species in areas of comparatively light periodic inundation but in much larger areas of an intermediate zone on the rather low but well-drained lands below the relatively higher zonal distribution of *H. guianensis* var. *lutea*. As has been pointed out in this paper, there is some morphological evidence that *H. brasiliensis*, as it exists on the *tierra altura*, is ecotypically and genetically different from that which grows on periodically inundated areas, probably having been evolved through introgression of *H. guianensis* var. *lutea* germ-plasm into *H. brasiliensis*.

Putative Hybrids in Peru

The occurrence in nature of interspecific hybridization in the genus *Hevea*, as evidenced from both wild and cultivated trees, is a fact which can neither be ignored nor questioned. Though intraspecific hybridization within *H. brasiliensis* has long been practiced as a means of *Hevea* improvement in the Far Eastern plantations (s'Jacob, 1931), it is not known accurately when the first artificial interspecific hybrids were produced.

One of the older recognized artificial hybrids is represented in the Herbarium of the Arnold Arboretum by a fine flowering specimen. It was collected at the Singapore Botanic Garden, December 17, 1923, by *Burkill s. n.*, is labeled *H. brasiliensis* × *confusa*, and includes notes concerning the two parents. A study of morphological characters shown by this specimen leaves little doubt but that this hybrid arose from a cross between *H. brasiliensis* and *pauciflora (confusa)*. It is of significance that this specimen matches remarkably well two specimens *(Seibert 1840* and *Kuhlman 1727)*, collected at Iquitos, Peru, which are of undoubted natural hybrid origin between the same species.

Ramaer (1935) has proved that artificial interspecific hybridization is possible between *H. brasiliensis* and *Spruceana*, and Schmöle (1938, 1941) has reported hybrids from this cross to be superior root stocks for budded clones of *H. brasiliensis* as tested at the A.V.R.O.S. General Experiment Station in Sumatra.

Pearson (1912) and Huber (1913) recognized that hybrid swarms existed between *H. brasiliensis* and *confusa* in the Botanic Garden and plantations in Trini-

dad. Huber then became quite conscious of certain floral and seed variations in trees around the low lands of the Amazon mouth region which appeared to him intermediate between *H. brasiliensis* and *H. Spruceana*. He recognized without doubt that hybridization was occurring between these two species and through comprehensive seed measurements suggested a method of selecting *H. brasiliensis* from *H. Spruceana* and resulting hybrids on the basis of seed size.

As Huber's successor, Ducke (1935, 1943) has devoted sections in his taxonomic works to the recognition and interpretation of natural hybrids occurring in the Amazon valley of Brasil. Furthermore, he has recognized that a number of named species and varieties are of hybrid origin. With additional opinions and evidence presented by La Rue (1926), Cook (1941), Schultes (1945), Baldwin (1946, 1947), and others, it has become necessary to include sections dealing with recognized hybrids in taxonomic works on *Hevea*.

Recognizable natural hybrids are morphologically distinguishable between many of the species and appear in general collections of *Hevea* from many parts of the Amazon valley. It appears that there are no strong genetic barriers between the species. If two or more species come together in their natural distribution and if natural conditions such as flowering time be favorable, natural hybridization may be expected to take place. If ecological conditions be naturally favorable or made favorable by man through clearing, planting, or pasturing, in such a way as to eliminate part or much of the strong natural selection found under normal jungle conditions, the hybridized seed may be expected to, and does, attain the status of mature, flowering and fruiting trees. In the jungle perhaps all but one out of a million seeds meet the fate of being eaten by animals; or, if seeds germinate, the seedlings are eaten by other animals; or the seedlings die within one to four months after germination due to lack of sufficient light on the forest floor. It is an extremely rare seedling which, due to a fallen jungle tree or being along a trail or clearing, ever attains maturity.

Hevea brasiliensis × guianensis var. lutea

Vernacular Names: *jebe debil-fino, shiringa debil-fino, jebe debil-fino de altura, shiringa itauba* (Peru).

Known Natural Distribution: Uusually on or near borders where the two species come together.

The specimens at hand rarely appear to be truly intermediate. In all cases it has been possible to note them as simulating more closely one or the other of the species. The following specimens appear most closely to simulate *H. guianensis* var. *lutea*:

Peru: dept. loreto: Rio Napo, Progreso, st. Oct. 1943, *Seibert 1840*. dept. puno: Upper Rio Inambari, valley of the Rio Huari-Huari, alt. 1000 m., st. May 1943, *Hodge 6013*. dept. madre de dios: Vic. Maldonado, south of Rio Tambopata (Seed progeny grown at Estación Experimental Agrícola de Tingo Maria), st. Jan. 1947, *Carpenter & Lescano s. n.* (P-127), fl. Sept. 1946, *s. n.* (P-128), st. Jan. 1947, *s. n.* (P-129). st. Jan. 1947, *s. n.* (P-130).

These specimens, through the presence of erect leaflets and pronounced short-shoots, are referable to *H. guianensis* var. *lutea.* Since most specimens represent selections from seed progeny obtained south of Maldonado, it is unfortunate that only one of these specimens is in flower, that of P-128. Here the flowers appear intermediate but lack the small calloused tips of *H. brasiliensis.* They have 6–8 anthers in two irregular whorls. The leaflets appear to be intermediate, but have the vein pubescence of *lutea.* As far as is known, the Hodge specimen was taken from a distance of about 175 kilometers from the nearest *H. brasiliensis.* If this be true, here is some interesting evidence of the distance to which introgression can penetrate into species distributions.

Hevea guianensis var. *lutea* is characteristic of the eastern slopes of the Peruvian Andean foothills where it occasionally reaches an altitude of 5000 feet. In the southern half of Peru it extends eastward into Bolivia south of the Rio Madre de Dios. Studies made from material originating near Maldonado show it to be superficially characteristic of *H. guianensis* var. *lutea*, but incorporating morphological features of *H. brasiliensis.*

Along the trail from Maldonado north to Iberia, a distance of 211 kilometers, there is a gap of some 50 kilometers between Maldonado and the Rio Manuripe in which *Hevea* scarcely exists. At the Rio Manuripe and to the north, *H. brasiliensis* occurs. From reports, this gap narrows at the Bolivian border east of Maldonado. There is little doubt but that the Maldonado *H. guianensis* var. *lutea* contains established germ-plasm of *H. brasiliensis.* It appears to have been derived through hybridization of the foothill *H. guianensis* var. *lutea* with the approaching *H. brasiliensis* characteristic of the adjoining northeastern Madre de Dios and northeastern Bolivia. In yield and rubber quality the Maldonado material is characteristically intermediate. The short-shoot character frequently is more or less intermediate; and the leaflets are often more horizontal than erect.

The following putative hybrid specimens appear most closely to simulate *H. brasiliensis:*

PERU: DEPT. HUANUCO: Rio Pachitea, Pto. Inca, old fr. Oct. 1945, *Seibert 2186.* DEPT. LORETO: Nauta, st. Nov. 1943, *Seibert & Russell 1881;* Iquitos, Estrada Morona, fl. Dec. 1942, *Baldwin 2829;* Rio Napo, Progreso, st. Oct. 1943, *Seibert 1847;* Rio Yavari, Islandia, st. Oct. 1940, *Skutch 4988.* DEPT. MADRE DE DIOS: vic. Maldonado, south of Rio Tambopata (from seed progeny grown at Estación Experimental Agrícola, Tingo Maria), st. Jan. 1947, *Carpenter & Lescano s. n.* (P-131).

BOLIVIA: DEPT. PANDO: Rio Tahuamanu, Porvenir, st. Dec. 23, 1923, *La Rue s. n.* DEPT. LA PAZ: Isapuri, st. Oct. 1901, *R. S. Williams 1658, 1659;* Mapiri, fl. Sept. 1939, *Krukoff 10824,* st. Sept. 1907, *Buchtien 1622;* Palmos, st. June 1902, *R. S. Williams 1657.*

These specimens appear to show the reclinate leaflets and inconspicuous short-shoots of *H. brasiliensis,* but the leaflets have the vein pubescence of *lutea.* Where flowers are present, the anthers are less than 10 in two irregular whorls. The flowers have intermediate acumination and the calyx lobes occasionally are without small calloused tips. All specimens appear to have been collected from areas above

periodic river inundation. Where it is known, the latex, though yellowish in color, is superior to that normally found in *lutea*.

The La Rue specimen from Porvenir, Bolivia, comes from a region in which *H. guianensis* var. *lutea* is not known. The nearest known occurrence of *lutea* is some 225 kilometers to the south and southwest. Here is a specimen from a center of supposedly pure *H. brasiliensis*, yet it shows *H. guianensis* var. *lutea* characters with little question, even to the inferior rubber and yellow latex. Though this specimen more clearly shows *H. guianensis* var. *lutea* influence than any other I have seen from the Pando-Madre de Dios area, it should be pointed out that *H. brasiliensis* trees with yellow latex and even inferior rubber are not too infrequent. Furthermore, some trees occasionally show slight intergrading characters in the flowers and leaves, discussed under *H. brasiliensis*. The indication is that the so-called Acre-Beni *H. brasiliensis* carries some slight *H. guianensis* var. *lutea* germ-plasm.

It is known that the seed which Sir Henry Wickham took from Brasil to inaugurate the development of the plantation rubber industry of the Far East came from the Tapajos River area near Boim, where the trees grow naturally on well-drained plateau land above any periodic inundation. Early impressions that *H. brasiliensis* grew on inundated land led to test plantings in the Far East on flooded land. It has long since been proved that the plantations did much better on land not subject to flooding, though the trees could live and grow if flooding were not over too long a period of time.

Is there any difference between *H. brasiliensis* from the *tierra baja* and that from *tierra altura*? There seems to be no difference sufficiently distinct to base taxonomic delimitation. Yet, there must be a genetic difference!

Repeated observations of trees and specimens from trees over the entire range of *H. brasiliensis*, and from the two types of habitat, have given some rather good morphological evidence that the *tierra altura*-loving *H. brasiliensis* has been derived through its incorporation of *H. guianensis* (or probably var. *lutea*) germ-plasm. It has been only through the detailed study of a relatively large number of specimens from the Tapajos, Matto Grosso, Acre, Bolivia, and Madre de Dios that certain otherwise unaccountable features sometimes crop up. An occasional specimen will show a tendency toward having a short-shoot. Rather frequently the midveins of the lower leaflet surface will show some pubescence. There may be a strong tendency here and there for the leaflets to approach a horizontal or semi-erect position. Position of the leaflets, one to another, is an interesting feature—varying from apart to touching and to overlapping. The overlapping condition is a rather constant feature of the *H. guianensis* complex. Much has been made of this variable character in clone identification work (Frey-Wyssling *et. al.*, 1932). Frequently, at least in seeds from the Madre de Dios, there is rather strong angularity, approaching the kite-shaped cross-section. Furthermore, there are occasional trees producing cream-colored and, more rarely, sulphur-yellow

latex. Again reference is made to a striking specimen (*La Rue s. n.*, Dec. 23, 1923, "*itauba*", from Porvenir, Bolivia), which combines several pronounced features of *H. guianensis* var. *lutea*. These features are rather conspicuous short-shoots, erect leaflets, and vein pubescence, all in the same specimen. Another specimen (*Seibert 2120*, Ultimatum, Peru-Bolivia border, near Iberia), has the male buds with only slight acumination plus pubescent leaflet veins. These two cases occur in the center of large areas in which only *H. brasiliensis* is represented. There is, it seems, no chance for direct hybridization to have taken place.

It would seem that the establishment of this "ecotype", which resulted from past hybridization, became relatively stabilized superficially as *H. brasiliensis* except for its habitat preference. However, it is still not sufficiently well established to prevent certain morphological throw-backs or recombinations resembling its minor constituent. It may well be referred to as a geographic race derived through ecotypic selection.

If in this discussion the true situation is approached, one can conclude that the plantation industry of the Far East is based not on pure strain *H. brasiliensis* but upon *H. brasiliensis* into which has been incorporated a slight amount of at least *H. guianensis* var. *lutea* germ-plasm.

Hevea brasiliensis × pauciflora

Vernacular Names: None typical of this group has been encountered in Peru.
Known Natural Distribution: Thus far it has been collected from the vicinity of Iquitos and Caballo Cocha.

Peru: dept. loreto: Iquitos: Marshy second growth on outskirts of city, fl. and fr. Dec. 1942, *Baldwin 2807*, fl., fr. *2810, 2811;* between Iquitos and Morona Cocha in old clearing along swampy stream, fl. Sept. 1944, *Seibert 1940*, fl. Oct. 1940, *Skutch 4903;* Punchana, marshy land, fl. Dec. 1942, *Baldwin 2817;* Mishuyacu, fl. Jan. 1930, *Klug 812.* Caballo Cocha: fl. Aug. 1929, *Llewelyn Williams 2503.*

The above Iquitos specimens are from an hybrid swarm, being most closely referable to *H. pauciflora* through the presence of the conspicuous calloused calyx lobe tips, dense, angular scales of the lower leaflet surface, peduncle departure, and seed characters. The varying degrees of bud and calyx lobe acumination, somewhat reclinate leaflets, and the continuous midvein to the end of the blade tips all show *H. brasiliensis* influence.

In these wild specimens there is not very good evidence of intergrading segregation from one species to the other, since they tend most closely to simulate *H. pauciflora*. The following cultivated specimens taken from a progeny growing at Hacienda Chanticlair on the edge of Iquitos give some experimental evidence that, where natural selection has to some extent been eliminated, there tends to be segregation of intergrading types from one to the other species.

dept. loreto: Hacienda Chanticlair, cultivated in garden, trees 12–20 m. tall, fl. and fr. Sept. 1943, *Seibert 1840*, fl. *1841, 1842, 1843*, fl. *1844*, fl. Mar. 1924, *Kuhlman 1527.*

On the outskirts of the city of Iquitos some 30 trees were planted about

twenty-five years ago from local seed in the garden of Hacienda Chanticlair. The trees show a beautiful series of segregational intermediates between *H. brasiliensis* and *H. pauciflora*, indicating them to be of hybrid origin. At the time of collection some of the trees were partially defoliating, others were in full flower, some with both flowers and maturing fruit, some with mature fruit, while still others were in sterile condition. In size they ranged from 10 to 20 m. tall. The trees had been tapped for a short time at the beginning of the war but tapping was abandoned because of the uniformly low yield of poor quality rubber, high in resin and turning blackish as is characteristic of *H. pauciflora*. The following table will attempt to demonstrate the morphological variations between the two species involved. It is unfortunate that more trees were not in flower at the time of collection to show the complete range of variation which was demonstrated by the group of trees as a whole.

HYBRID SWARM *H. BRASILIENSIS* × *PAUCIFLORA*, HACIENDA CHANTICLAIR, IQUITOS

	Pistillate disk lobes	Pistillate calyx lobe contortion	Pistillate bud contortion	Staminate disk	Staminate calyx lobe contortion	Staminate bud contortion	Staminate bud acumination	Midvein tip	Scales	Leaf persistence	Short-shoots
H. brasiliensis	0*	5	5	0	5	5	5	Continuous, not calloused	Round	0	0
Seibert 1840	5	2	1	2	2	0	2	Continuous, calloused	Intermediate	3	4
Seibert 1841	2	5	5	1	5	3	5	Continuous, not calloused	Round	0	5
Seibert 1842	0	?	?	?	?	?	?	Continuous, calloused	Round	0	0
Seibert 1843	3	3	2	2	0	0	2	Continuous, not calloused	Round	0	0
Seibert 1844	1	5	5	2	2	3	4	Continuous, calloused	Round	0	0
Kuhlman 1727	?	?	?	3	4	2	5	Continuous, calloused	Angular	3	4
H. pauciflora	5	0	0	5	0	0	0	Short of tip, calloused	Angular	5	5

*The numbers represent relative degrees to which the character is pronounced.

The group of trees is not only characterized by having very poor rubber, but is relatively free of South American Leaf Blight, *Dothidella Ulei*, a character which appears to be, in the Iquitos region, more inherent in *H. pauciflora* as a whole than in *H. brasiliensis*. This meager evidence would indicate some link between poor quality and low latex yield.

HEVEA GUIANENSIS × PAUCIFLORA

VERNACULAR NAMES: *shiringa bananera, jebe debil muerto* (Peru).

KNOWN NATURAL DISTRIBUTION: Southwestern Colombia, western Brasil, eastern north-central Peru.

PERU: DEPT. LORETO: Iquitos: Estrada Morona, outskirts of city, fl. and fr. Dec. 1942, *Baldwin 2829-A*; Punchana, hillside in old second growth near stream, st. Feb. 1944, *Seibert 2269*. Rio Napo: Curaray, st. Oct. 1940, *Skutch 4986*; 40 kilometers above mouth of Rio Napo, low hills away from river, fl. and old fr. Oct. 1943, *Seibert 1851*.

Although morphologically referable to *H. guianensis* in nearly all respects, the lepidote condition of the lower leaflet surface approaches that found in *H. pauciflora*. The rubber from these trees is extremely poor. It does not retain its shape in ball form after smoking, but rather flattens out, even overnight. The yellowish tan, resiny latex soon oxidizes black to appear as stains on clothing characteristic of banana juice stains—thus the vernacular name, *bananera*. Too little material from Peru is available for thorough study, either from the standpoint of distribution or segregational variability.

Hevea guianensis var. *marginata* is questionably known from Peru, by a collection made by Skutch *(No. 4986)* from Curaray, Rio Napo. Many specimens of this variety from Manaos have been examined and found to have the lepidote condition and, on rare occasions, the disk development of *H. pauciflora*. The somewhat revolute leaflet edges appear superimposed on what otherwise seems to be *H. guianensis* with obovate leaflets, rounded at the tip. In these characters (disk is not known) and in superficial aspect the Peruvian collection agrees. It would appear that the development of *H. guianensis* var. *marginata*, through introgression of *H. pauciflora* into *H. guianensis*, should be taken into consideration. The Manaos material indicates that the more or less stable entity has been derived through hybrid origin.

HEVEA GUIANENSIS var. LUTEA × BENTHAMIANA

H. Foxii Huber, in Bol. Mus. Goeldi 7:228. 1913.
H. glabrescens Huber, l. c., p. 230, in part.

VERNACULAR NAMES: *ituri* (Peru).

KNOWN NATURAL DISTRIBUTION: Rio Putumayo, Peru-Colombia border and Rio Maranon.

PERU: DEPT. LORETO: Rio Putumayo: Liberia, fl. and fr. Feb. 1911, *Fox s. n.* (SYNTYPE of *H. glabrescens* Huber); Ultimo Retiro, fl. and fr. Oct. 1910, *Fox 7* (TYPE of *H. Foxii* Huber). Rio Marañon: Santa Rosa near Pinglo, st. May 14, 1943, *Russell s. n.*

These specimens morphologically are most closely allied to *H. guianensis* var. *lutea*, with its distinct short-shoot, lack of disk lobes, and very irregular anther whorls. In Fox's Liberia specimen, the anthers are of two sizes, two approaching 1 mm. in length, the others about 0.5 mm. However, these characters are complicated by leaflet pubescence, long reddish floral pubescence, and the bud and calyx lobe acumination, which are definitely characters of *H. Benthamiana*.

Two specimens of Huber's *H. glabrescens* were cited in the original description. Both these Fox collections from Sombra and from Pebas appear to me to be better placed in *H. guianensis* var. *lutea* × *pauciflora*.

It is unfortunate that the Russell specimen from the Rio Marañon is sterile, preventing accurate placement. It is such an unusual specimen that superficially some might think it to be a new species. The presence of short-shoots and other characters indicates to me that it is allied to *H. guianensis* var. *lutea*, but the pubescence of the lower leaflet surfaces is extremely dense, as dense as in the most typical of *H. Benthamiana* specimens. The pubescence, however, is white, a character not too often found in good *H. Benthamiana*. With the exception of *H. Benthamiana*, reported found on the Peru border on the lower Putumayo, *H. Benthamiana* appears actually never to have been collected in Peru, much less as far up on the Marañon as Pinglo. The question arises as to how *H. Benthamiana* characters can arise in *H. guianensis* var. *lutea* specimens so far away from *H. Benthamiana* range. Either *H. Benthamiana* exists along the Peruvian Amazon and Marañon and has been overlooked, or *H. guianensis* var. *lutea* is carrying *H. Benthamiana* germ-plasm which occasionally recombines in certain specimens to show itself rather strongly, as in the Russell specimen. This latter theory at present appears plausible to me. Through comparative morphological studies of the flowers, leaves, stems and short-shoots, and through the great amount of segregational-like variability of *H. guianensis* var. *lutea*, I feel that it may have been derived through interspecific hybridization of *H. guianensis* and *H. Benthamiana*.

According to Fox's notes published with Huber's description, *H. Foxii* produced 75 per cent of the rubber of the Putumayo. This region was again in production during the past war, from which came the "Putumayo Block" and "*rabos de Putumayo*[34]" grades of rubber slightly superior to normal *H. guianensis* var. *lutea*. This better quality rubber, as well as morphological characters, would indicate that the *H. guianensis* var. *lutea* of the Putumayo may have incorporated some of the *H. Benthamiana* rubber quality and more of the other *H. Benthamiana* tendencies than is generally found in other regions.

HEVEA GUIANENSIS var. LUTEA × PAUCIFLORA

H. glabrescens Huber in Bol. Mus. Goeldi 7:230. 1913, in part.

In morphological aspect the following specimens are most closely referable to *H. guianensis* var. *lutea*:

VERNACULAR NAMES: *jebe debil, jebe debil debil, jebe debil bananera* (Peru).

KNOWN NATURAL DISTRIBUTION: *Tierra altura*, probably in secondary growth, scattered along the Rio Putumayo and the Rio Amazonas, from Iquitos to Caballo Cocha.

PERU: DEPT. LORETO: Rio Putumayo: Sombra, fr. Dec. 24, 1910, *Fox s. n.* (SYNTYPE of *H. glabrescens* Huber). Rio Amazon: Rio Nanay, Tierra Doble, st. June 1929,

[34] Literally translated from the Spanish as "Putumayo tails," used during the past rubber boom as a term describing tail-like appearing masses in the classification of a rubber from that region of Peru. These so-called "Putumayo tails" are made up of scrap rubber, taken from the tapped trees, and is wrapped into shapes simulating tails. Before the use of the more modern tapping knives came into effect, trees were tapped with a small hatchet known as the *machadiño*. In the Putumayo area, coagulated rubber from these wounds was placed in a crude press to form huge masses or "blocks" of rubber, known as "Putumayo blocks."

Llewelyn Williams 918, Pebas, st. Mar. 4, 1911, *Fox s. n.* (PARATYPE of *H. glabrescens* Huber); Caballo Cocha, Quebrada Mazamore Cana, st. Oct. 1943, *Seibert 1867*, fl. *1868*.

These specimens all show remarkable similarity to the one syntype of *H. glabrescens* collected by Fox at Sombra on the Rio Putumayo. They are referable to *H. guianensis* var. *lutea*. However, the way in which the peduncle departs horizontally from the short-shoot and hangs down, the short-shoots, leaflet persistence, and the lepidote condition of the under-leaflet surfaces all show *H. pauciflora* tendencies. The latex and rubber quality are poor and as ascribed to *H. guianensis* × *pauciflora*.

The following specimens are most closely referable to *H. pauciflora*, with indications that they are members of an hybrid swarm in which segregation and natural selection are such as to produce types most closely simulating *H. pauciflora*.

H. paludosa Ule, in Engl. Bot. Jahrb. 35:666. 1905.
H. humilior Ducke in Archiv. Jard. Bot. Rio de Janeiro 5:154, *pl. 20, fig. 50*. 1930.

KNOWN NATURAL DISTRIBUTION: On *tierra altura*, but on the edges and near local marshy areas of pasture land containing second growth and in second growth in the vicinity skirting Iquitos (pl. 44).

PERU: DEPT. LORETO: Iquitos: Estrada Morona, marshy land, outskirts of city, fl. Nov. 1942, *Baldwin 2812, 2813*, fl. and fr. *2814;* road to Morona Cocha, fr. Nov. 1945, *Ducke 1774*, fl. and fr. Oct. 1927, *Ducke 20602* (SYNTYPE-2 of *H. humilior* Ducke), fl. March 1924, *Kuhlman 1526* (Jard. Bot. Rio *No. 2411*), (SYNTYPE-1 of *H. humilior* Ducke), fl. July 1902, *Ule 6260* (TYPE of *H. paludosa* Ule); vic. Punchana, fl. and fr. Sept. 1943, *Seibert 1838*, fl. *1839;* San Juan, st. Dec. 1942, *Baldwin 2819;* Mishuyacu, fl. Oct.-Nov. 1929, *Klug 128*.

These trees, up to 20 m. in height, appear to have a variable range of flowering time. From the presence of both maturing fruit and flowers on the same tree, it would seem that the trees may flower more than once a year. There is some bud acumination, usually an irregularity of the anther whorls, less than 10 anthers, and a reddish tinge to the floral pubescence—all indications of *H. guianensis* var. *lutea*. The calyx lobes always show calloused tips, the peduncle departs at right angles from the stem and droops, and the vein tips are usually calloused and stop short of the blade tip—all strongly indicating *H. pauciflora*. The leaflet scales intergrade between the type of the two entities. The rubber, where known, is always very poor and resinous, turning black when drying.

As in the case of Kuhlman's syntype of *H. humilior*, it is not always too easy to distinguish morphological characters of *H. guianensis* var. *lutea* except in a rather vague way through pubescence characters. Furthermore, the leaflets tend to be more horizontal than erect, so strongly do these members of the hybrid swarm tend towards *H. pauciflora*.

HEVEA GUIANENSIS var. LUTEA × PAUCIFLORA × BRASILIENSIS

PERU: DEPT. LORETO: Rio Ampiyacu, Puca Orquillo, fl. and young fr. Oct. 1943, *Seibert 1862*.

This specimen has caused me considerable concern because it shows morpho-

logical influence of all three species, but, in general, it perhaps most closely simulates *H. guianensis* var. *lutea* on the basis of the erect leaflets, the short-shoots, 8 or less anthers in two whorls, and the vein pubescence of the lower leaflet surfaces. The inflorescence is intermediate between *H. pauciflora* and *H. brasiliensis* while the way in which the peduncle of the young infructescence departs from the stem is that of *H. pauciflora*. The leaves, which persist until after inflorescence maturation and the appearance of the new flush, appear as those found in *H. pauciflora*. The flowers, through acumination and pubescence, are superficially those of *H. brasiliensis*, even to the slight bud contortion. The calyx lobes lack the calloused tips of either *H. brasiliensis* or *pauciflora*. The presence of disk lobes in the pistillate flower simulates those of *H. pauciflora*. The leaflets are quite intermediate between *H. guianensis* var. *lutea* and *H. brasiliensis*. It is interesting to note that the male buds always absciss before anthesis. Perhaps this is a type of male sterility.

The tree was rather small, 15 m. tall, growing on a low hillside well above inundation level. It came from an area where *H. guianensis* var. *lutea* predominates and is known as *jebe debil fino de altura*, yet the rubber from this tree appeared to be quite inferior. The cream-colored latex stains the hands red before rapidly oxidizing to black. This blackish oxidation of the latex is a character which in my experience always shows up where admixture of *H. pauciflora* is suspected.

ECONOMIC ASPECTS OF CURRENT INVESTIGATIONS

Langford (1945) has shown that within the native habitat of the commercially grown *H. brasiliensis* there are strains which naturally resist the virulent South American Leaf Blight, *Dothidella Ulei* P. Henn. Notably resistant strains have been found to exist in the Acre territory of Brasil and from the Leticia region of Colombia on the Peruvian border. More recent studies have included the region of northeastern Madre de Dios, Peru, within the range of resistant *H. brasiliensis* strains.

Living material from these areas is now being grown and tested at various Latin American cooperative experiment stations, on the basis of which it is now possible to develop a sound industry of commercially grown rubber in this hemisphere. Since the South American Leaf Blight exists in many of the Latin American countries and threatens to spread to those in which it has not yet been reported, the development of this natural rubber industry is being based on material naturally resistant to the disease.

Although clones of *H. brasiliensis* have been developed in the Far East which have proved to be of superior yield, none of them have withstood resistance tests against this disease. As a temporary means of utilizing the high-producing, but susceptible, Oriental Clones in the trial plantings within this hemisphere it is necessary to top- or crown-bud these plants with indigenous clones of proven

resistance to the Leaf Blight (Sorensen, 1942). Clones for top budding may include resistant strains of other species than *H. brasiliensis*.

Thus far, time has been a limiting factor in testing and proving yield potentialities of more than a comparatively few of the earlier-found resistant clones. It would seem likely that through large-scale testing of many jungle-selected clones, particularly from superior yielding trees from such promising areas as Madre de Dios and adjoining Acre and Pando, a number of clones will prove to have naturally inherent characteristics of combined superior yield and high resistance. Seedling progeny from seed collected in such areas are growing to maturity at various stations. From these progeny further desired selections may be made and may prove even better than actual individual jungle selections. In addition to these methods of obtaining desirable planting material for Latin America, a breeding program is under way. By artificial breeding it is possible to utilize and combine desired characters of many clones. It is necessary that these clones meet specified requirements of many localities throughout Latin America where the growing of *Hevea* as an additional small farm cash crop would be of benefit to the community.

Hevea brasiliensis, as we are beginning to understand it throughout its very large range in the Amazon Valley, is an extremely variable species. It is variable not only in its morphology, but in its habitat preferences, altitudinal range, dry-season tolerance, disease resistance, latex yield, rubber quality and many other specialized features. It becomes apparent along modern lines of genetic thought that within this species itself are the basic ingredients for breeding artificial clonal material suitable to many of the varied conditions found throughout Latin America. For example, the fact that dense human populations and small-farm communities are more or less confined to elevations above the hot, insect-infested lowlands in which *Hevea* is considered to grow best, need not mean that human populations must be moved to *Hevea*-growing areas. It should be the aim, since high-elevation stock is available, to develop *Hevea* so it can be taken to the populations existing between 2000 and 4000 feet, or even higher.

Though natural hybrids between many of the species are recognized, we do not know much more about them than that there appear to be few genetic barriers between the various species.

No species has yet been found to have superior yield of rubber to that of *H. brasiliensis*. Where known, hybrids between it and any other species appear to result in a considerable lowering of qualities which are of prime commercial importance. Indiscriminate or promiscuous interspecific hybridization, if not controlled, could well lead to expenditures of huge sums of money and disastrous results. There are, however, a number of features of some other species such as exceptional disease resistance in strains of *H. pauciflora* and certain other species, the xerophytic nature of some forms of *H. nitida*, and many others which hold an interesting problem of interspecific hybridization for the plant breeder in the improvement of plantation *Hevea*.

List of Peruvian and Bolivian Specimens Studied

Archer, W. A. *7582 (H. nitida); 7583 (H. guianensis* var. *lutea).*

Baldwin, J. T., Jr. *2800, 2801, 2802, 2803, 2805, 2806 (H. pauciflora); 2807 (H. brasiliensis × pauciflora); 2808, 2809 (H. pauciflora); 2810, 2811 (H. brasiliensis × pauciflora); 2812, 2813, 2814 (H. guianensis* var. *lutea × pauciflora); 2815, 2816 (H. pauciflora); 2817 (H. brasiliensis × pauciflora); 2818 (H. pauciflora); 2819 (H. guianensis* var. *lutea × pauciflora); 2820 (H. pauciflora); 2821 (H. brasiliensis); 2822, 2823, 2824, 2826, 2827 (H. guianensis* var. *lutea); 2828 (H. brasiliensis); 2829 (H. brasiliensis × guianensis* var. *lutea); 2829-A (H. guianensis × pauciflora); 2830 (H. pauciflora); 2955, 2957 (H. brasiliensis); 2961 (H. guianensis* var. *lutea); 2998 (H. brasiliensis).*

Buchtien, Otto. *1622 (H. brasiliensis × guianensis* var. *lutea).*

Carpenter, J. B., & Manuel Lescano. *s. n.* P-A[35], P-B, P-1, P-24, P-25, P-26, P-36, P-39, P-52, P-56, P-58, P-65, P-66, P-67, P-69, P-73, P-76, P-77, P-78, P-80, P-81, P-83, P-84, P-85, P-86, P-87, P-88, P-90, P-91, P-99 *(H. brasiliensis);* P-127, P-128, P-129, P-130, P-131 *(H. brasiliensis × guianensis* var. *lutea);* P-142 *(H. brasiliensis);* P-143 *(H. brasiliensis × ?nitida);* P-145, P-146, P-147 *(H. brasiliensis);* P-151, P-153 *(H. guianensis* var. *lutea).*

Ducke, Adolfo. *1774 (H. guianensis* var. *lutea × pauciflora); 20598 (H. guianensis* var. *lutea); 20602 (H. guianensis* var. *lutea × pauciflora).*

Fletcher, Claude. *s. n. (H. brasiliensis); s. n. (H. guianensis* var. *lutea).*

Fox, W. 7, Herb. Rio *11845 (H. guianensis* var. *lutea × Benthamiana);* Herb. Rio *11847 (H. guianensis* var. *lutea × pauciflora);* Herb. Rio *11848 (H. guianensis* var. *lutea × Benthamiana);* Herb. Rio *11849 (H. guianensis* var. *lutea × pauciflora).*

Hodge, W. H. *6013 (H. brasiliensis × guianensis* var. *lutea).*

Huber, J. *1377 (H. guianensis* var. *lutea); 1534 (H. nitida).*

Killip, E. P., & A. C. Smith. *25406 (H. brasiliensis × H. guianensis* var. *lutea); 28706 (H. guianensis* var. *lutea); 29919 (H. pauciflora).*

Klug, G. *128 (H. guianensis* var. *lutea × pauciflora); 812 (H. brasiliensis × pauciflora).*

Krukoff, B. A. *1628 (H. nitida); 10824 (H. brasiliensis × guianensis* var. *lutea).*

Kuhlman, J. G. *1526 (H. guianensis* var. *lutea × pauciflora); 1527 (H. brasiliensis × pauciflora).*

Langemack, Victor. *s. n. (H. guianensis* var. *lutea).*

La Rue, C. D. *s. n. (H. brasiliensis); s. n. (H. brasiliensis × guianensis* var. *lutea); s. n. (H. guianensis* var. *lutea).*

Rusby, H. H. *885 (H. brasiliensis).*

Russell, Raymond. *s. n. (H. brasiliensis); s. n. (H. guianensis* var. *lutea); (H. guianensis* var. *lutea × Benthamiana).*

Seibert, R. J. *1838, 1839 (H. guianensis* var. *lutea × pauciflora); 1840, 1841, 1842, 1843, 1844 (H. brasiliensis × pauciflora); 1847 (H. brasiliensis × guianensis* var. *lutea); 1848 (H. guianensis* var. *lutea); 1849 (H. brasiliensis × guianensis* var. *lutea); 1850 (H. guianensis* var. *lutea); 1851 (H. guianensis × pauciflora); 1853 (H. brasiliensis); 1854 (H. guianensis* var. *lutea × pauciflora); 1855, 1856, 1857 (H. guianensis* var. *lutea); 1861 (H. brasiliensis); 1862 (H. guianensis* var. *lutea × pauciflora × brasiliensis); 1864 (H. brasiliensis); 1867, 1868 (H. guianensis* var. *lutea × pauciflora); 1869, 1872, 1873, 1874, 1876, 1877, 1882, 1883, 1884, 1893, 1904, 1905, 1923, 1925, 1926, 1932, 1933, 1934, 1935, 1936, 1937, 1938, 1939 (H. brasiliensis); 1940 (H. brasiliensis × pauciflora); 1943 (H. guianensis* var. *lutea); 1944, 1955, 1956, 1957, 1958, 1959, 1960, 1961, 1962, 1963, 1964; 1965, 1974, 1975 (H. brasiliensis); 1978 (H. guianensis* var. *lutea); 2021, 2023, 2024, 2025, 2026, 2027, 2028, 2030, 2031, 2032, 2033, 2053, 2060, 2062, 2065 (H. brasiliensis); 2074, 2078 (H. guianensis* var. *lutea); 2082 (H. brasiliensis); 2087 (H. guianensis* var. *lutea); 2091, 2102, 2105, 2106, 2115, 2116, 2120, 2130, 2141, 2142, 2143,*

[35] Collectors' number lacking, these being references to the clone number of the plant collected. The clones represent jungle selections from Peru cultivated at the Estación Experimental Agricola de Tingo Maria, Peru, where they are undergoing experimental testing.

2144 (H. brasiliensis); 2184, 2185 (H. guianensis var. *lutea); 2186 (H. brasiliensis* × *guianensis* var. *lutea); 2234, 2236, 2261, 2262 (H. guianensis* var. *lutea); 2269 (H. guianensis* × *pauciflora); 2370, 2371, 2404, 2406, 2407, 2426 (H. guianensis* var. *lutea).*

Seibert, R. J., & Manuel Lescano. *2270, 2271, 2272, 2273, 2274, 2275, 2276, 2277, 2278, 2279, 2280, 2281, 2282, 2283, 2284, 2285, 2286, 2287, 2288, 2289, 2290, 2291 (H. brasiliensis).*

Seibert, R. J., & Raymond Russell. *1881 (H. brasiliensis* × *guianensis* var. *lutea).*

Skutch, A. F. *4963, 4966, 4974 (H. guianensis* var. *lutea); 4976 (H. brasiliensis* × *guianensis* var. *lutea); 4980, 4981, 4983 (H. guianensis* var. *lutea); 4984 (H. brasiliensis); 4985 (H. guianensis); 4986 (H. guianensis* × *pauciflora); 4987 (H. brasiliensis); 4988 (H. brasiliensis* × *guianensis* var. *lutea); 4990, 4991, 4992 (H. pauciflora); 4993 (H. brasiliensis* × *pauciflora).*

Ule, E. *6260 (H. guianensis* var. *lutea* × *pauciflora).*

White, O. E. *2378 (H. brasiliensis).*

Wier, J. R. *s. n. (H. brasiliensis).*

Williams, Llewelyn. *206 (H. brasiliensis); 818 (H. guianensis* var. *lutea); 889 (H. nitida); 918 (H. guianensis* var. *lutea* × *pauciflora); 2003, 2176 (H. brasiliensis); 2503 (H. brasiliensis* × *pauciflora); 2931 (H. brasiliensis).*

Williams, R. S. *1657, 1658, 1659 (H. brasiliensis* × *guianensis* var. *lutea).*

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* Valid names are in Roman type, synonyms in *italics*.

EXPLANATION OF PLATE

PLATE 32

Fig. 1. *Hevea brasiliensis.* Terminal and lateral branch growth intervals or "flushes", separated by a narrow ring of bud-scale scars.

Fig. 2. *Hevea pauciflora.* Terminal and lateral branch growth intervals or "flushes", separated by a conspicuous "interflush" short-shoot region. Note the conspicuous lateral spur development preceding long-shoot or "flush" development.

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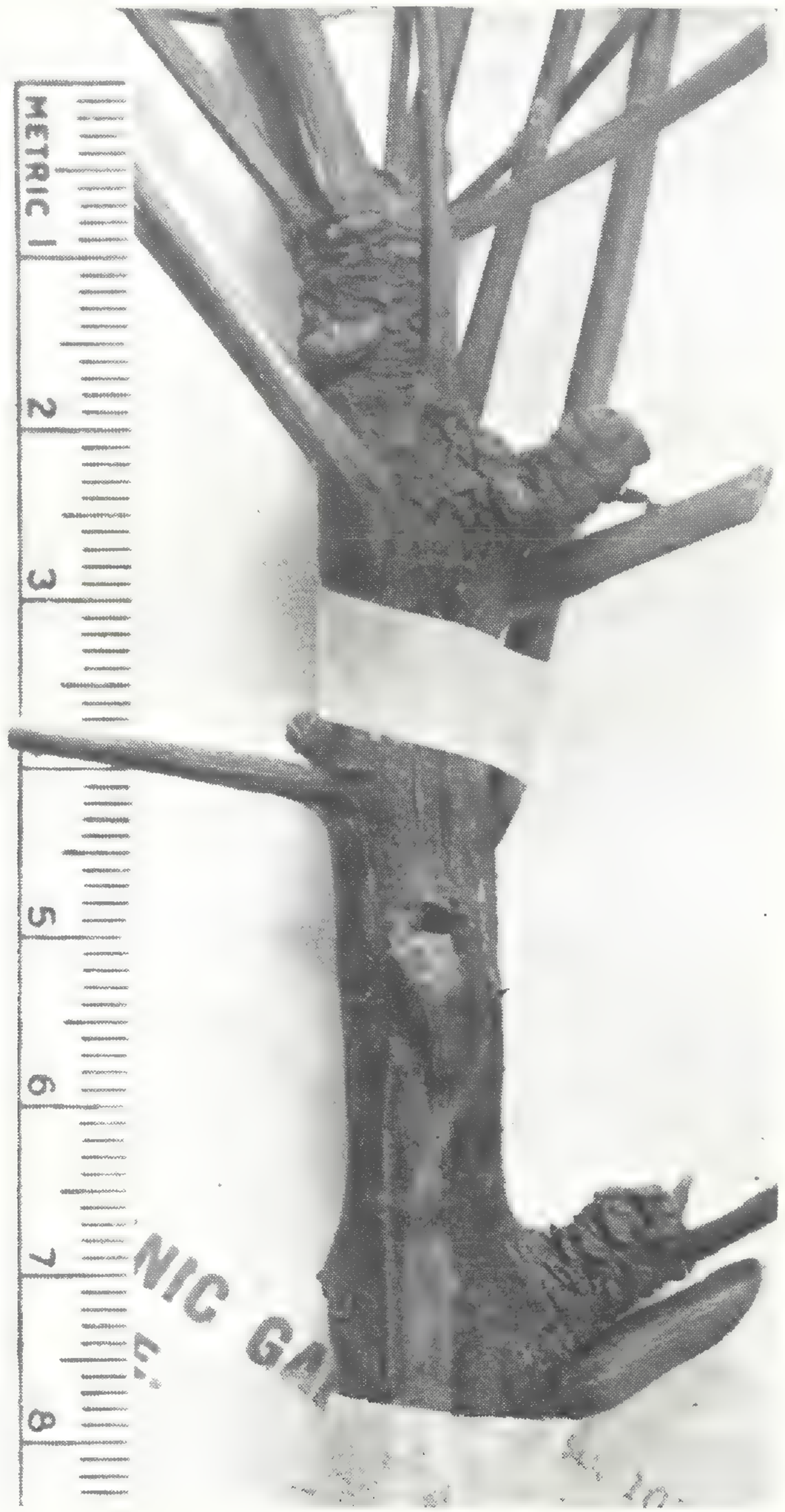

2

Explanation of Plate

PLATE 33

Fig. 1. *Hevea guianensis.* Terminal bud scales and conspicuous development of the short-shoot before the appearance of the inflorescence.

Fig. 2. *Hevea Spruceana.* Terminal bud scales and the short-shoot from which the inflorescence arises.

Fig. 3. *Hevea guianensis.* Three "interflush" short-shoots, from the youngest of which the inflorescence arises. Note the two "flush" regions, upon the upper of which the leaves remain persistent even after the appearance of the new inflorescence.

1

2

3

Explanation of Plate

PLATE 34

Fig. 1. *Hevea brasiliensis*. Complete leaf defoliation of the previous "flush" before the appearance of the inflorescence and new "flush".

Fig. 2. *Hevea rigidifolia*. Complete leaf persistence of the previous "flush" even after the appearance and maturation of the inflorescence.

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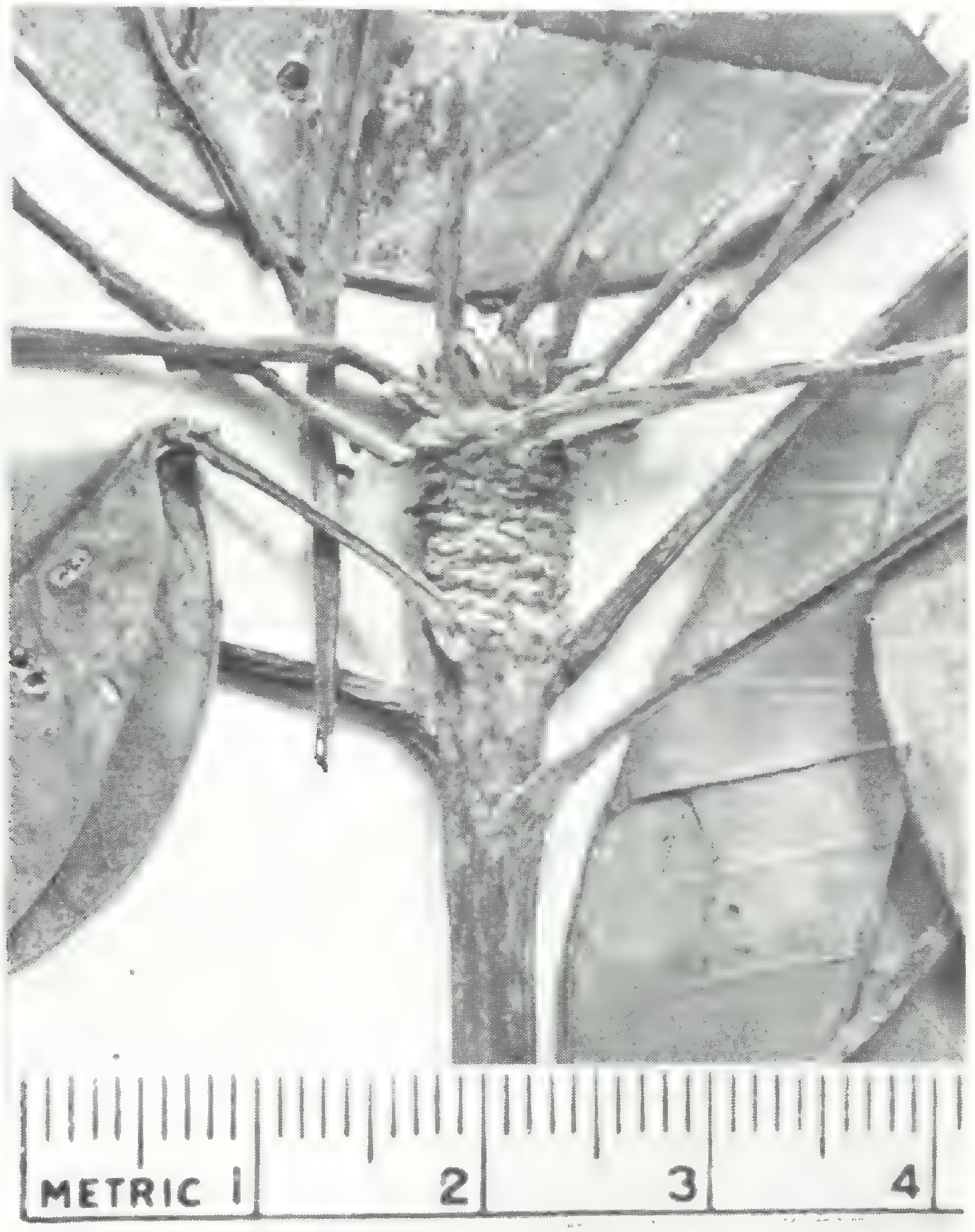

2

Explanation of Plate

PLATE 35

Fig. 1. *Hevea guianensis.* Staminate bud, open and dissected flowers; pistillate bud, open and dissected flowers.

Fig. 2. *Hevea guianensis* var. *lutea.* Staminate bud, open and dissected flowers; pistillate bud, open and dissected flowers.

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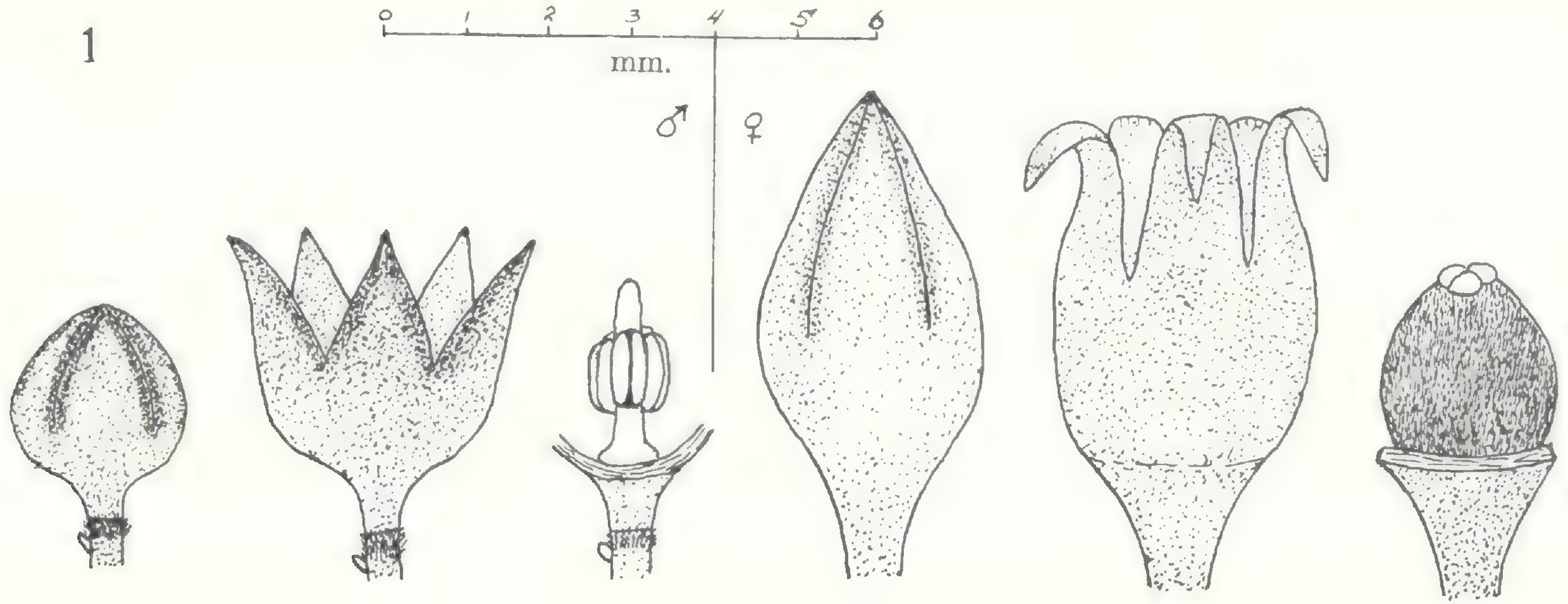

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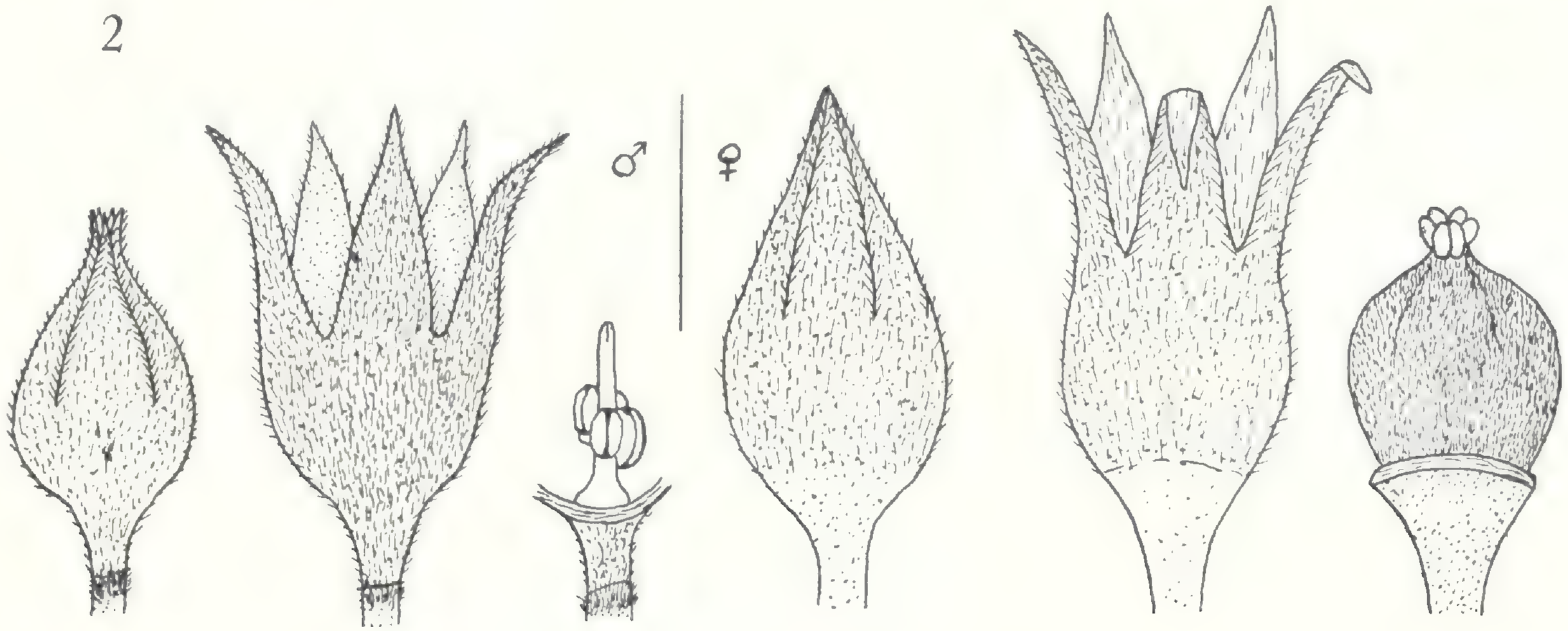
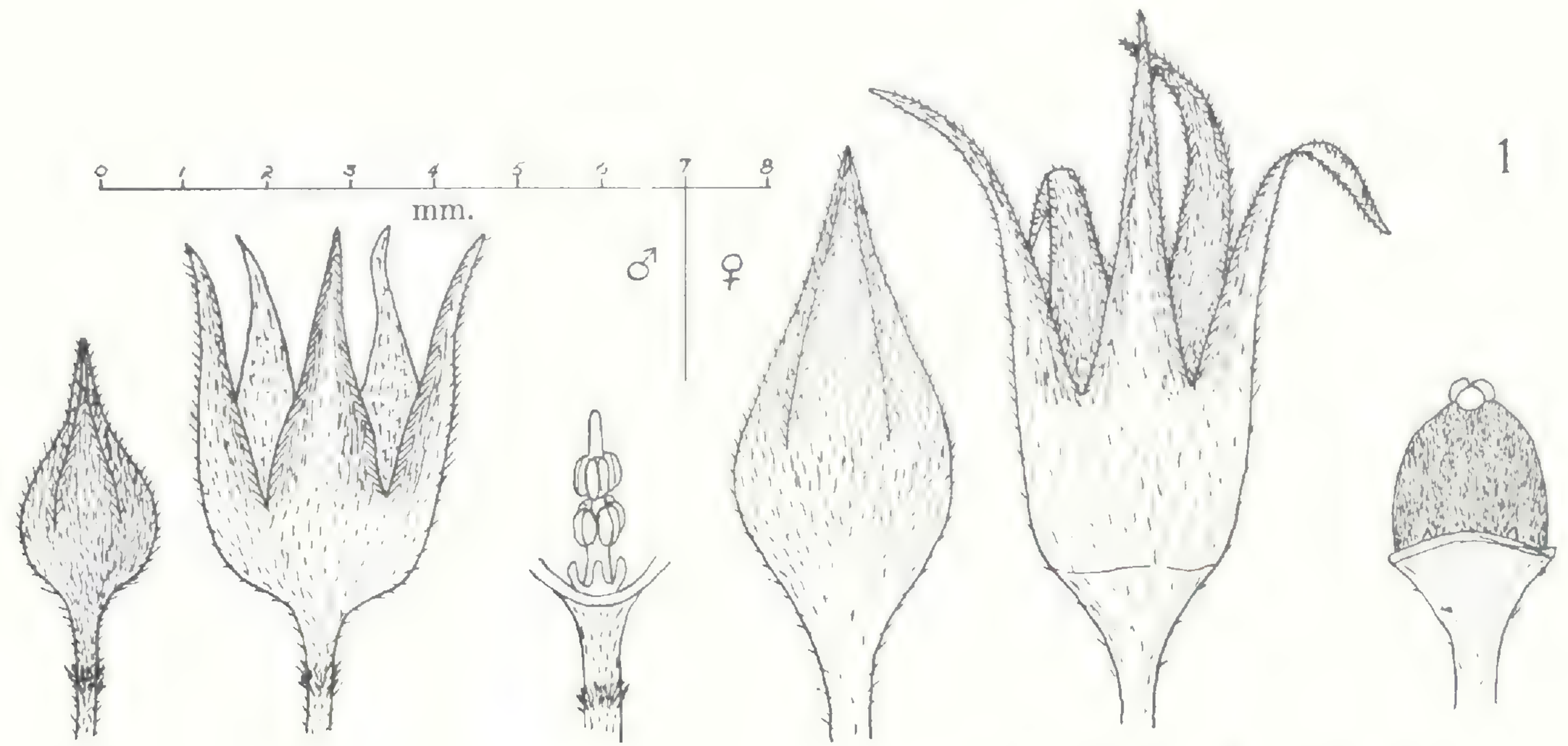


Explanation of Plate

PLATE 36

Fig. 1. *Hevea Benthamiana*. Staminate bud, open and dissected flowers; pistillate bud, open and dissected flowers.

Fig. 2. *Hevea Spruceana*. Staminate bud, open and dissected flowers; pistillate bud, open and dissected flowers.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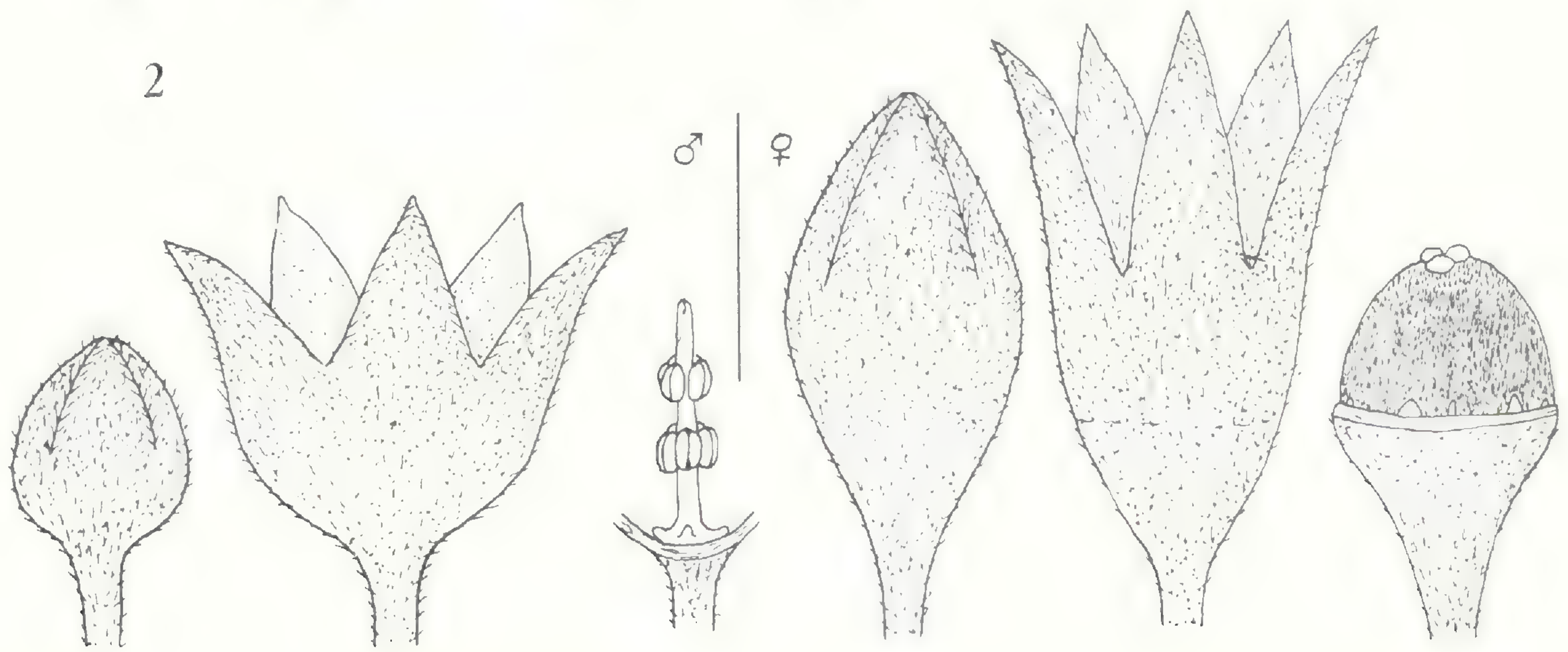
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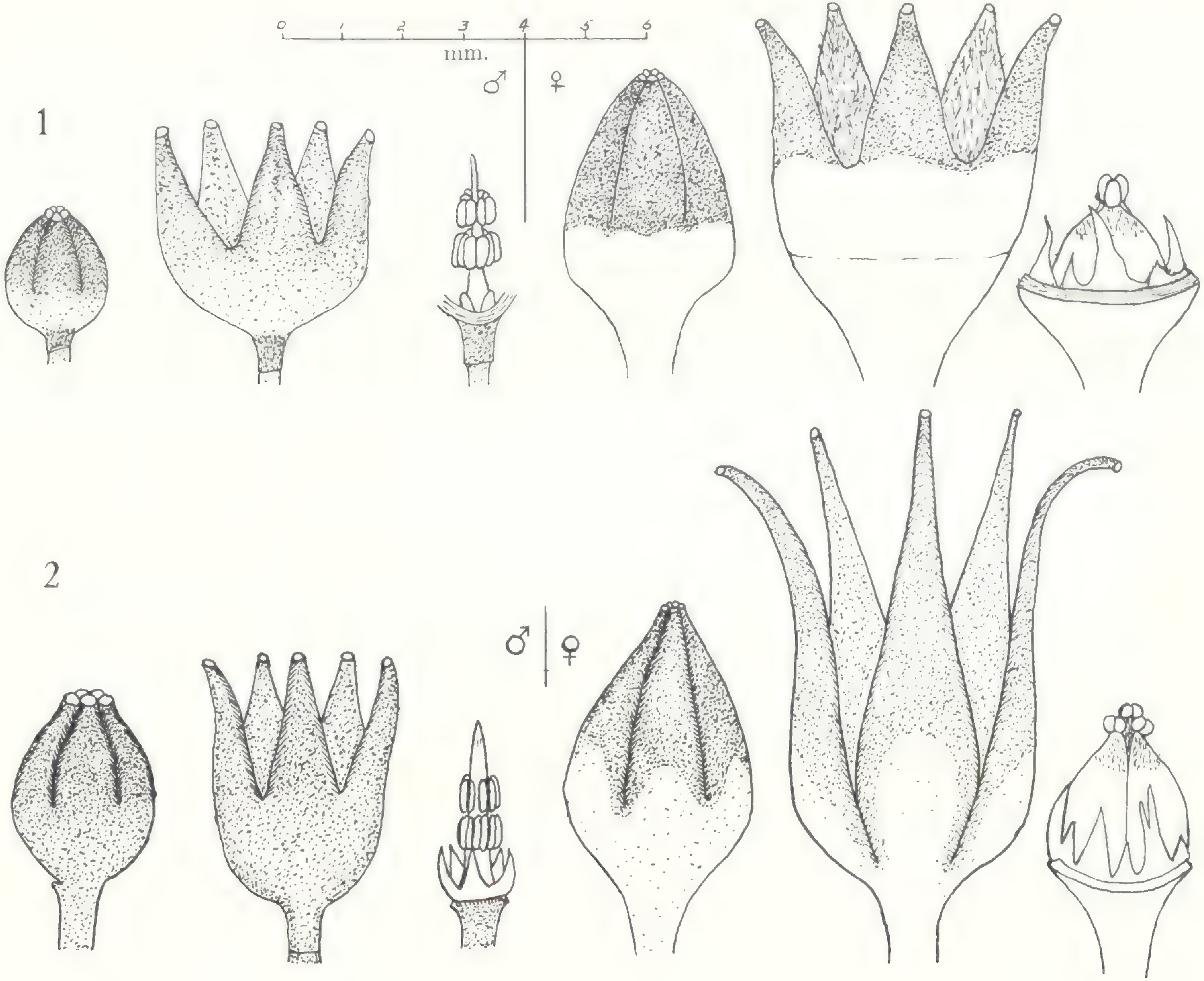
Explanation of Plate

PLATE 37

Fig. 1. *Hevea pauciflora.* Staminate bud, open and dissected flowers; pistillate bud, open and dissected flowers.

Fig. 2. *Hevea nitida.* Staminate bud, open and dissected flowers; pistillate bud, open and dissected flowers.



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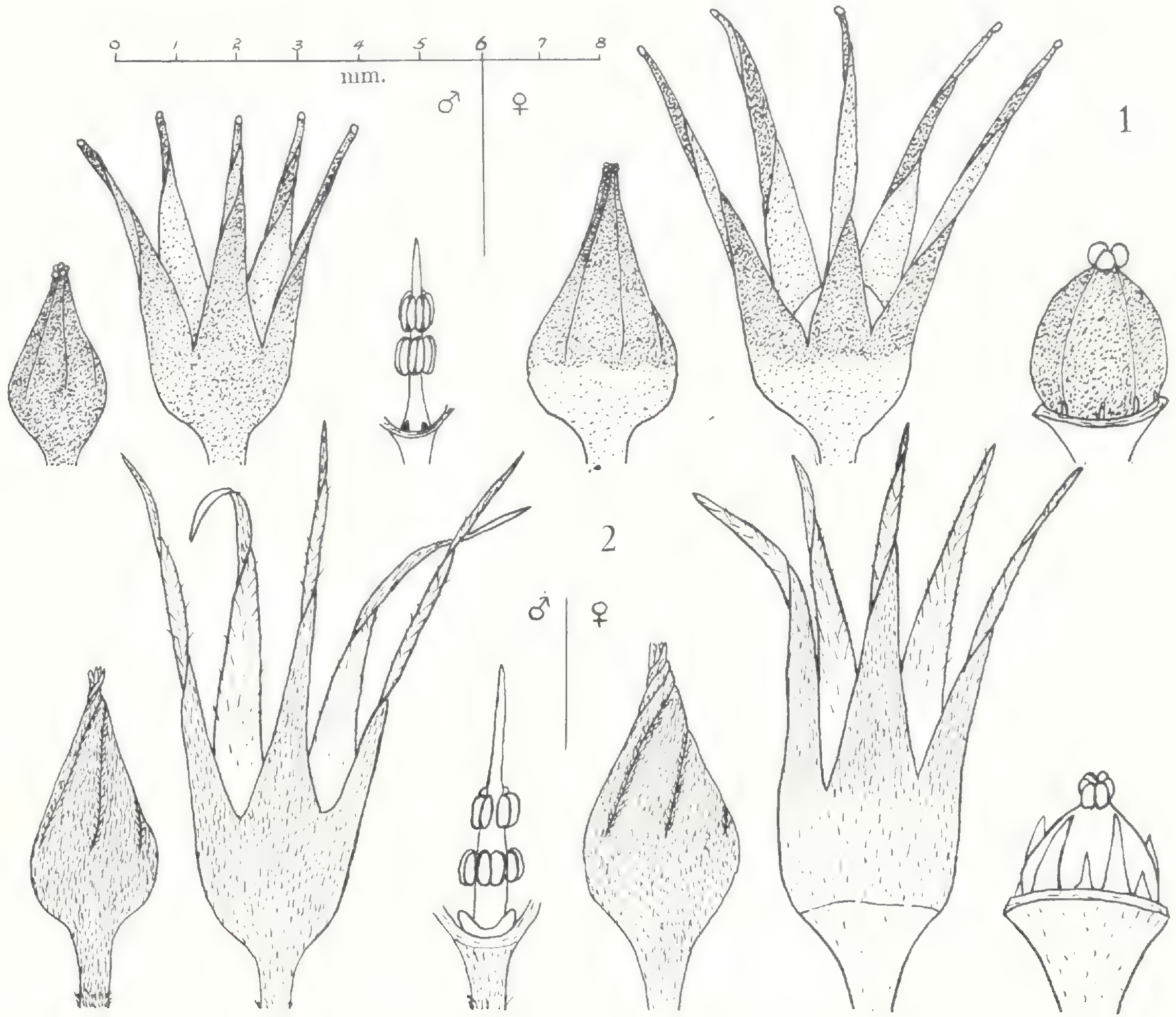
Explanation of Plate

PLATE 38

Fig. 1. *Hevea brasiliensis.* Staminate bud, open and dissected flowers; pistillate bud, open and dissected flowers.

Fig. 2. *Hevea rigidifolia.* Staminate bud, open and dissected flowers; pistillate bud, open and dissected flowers.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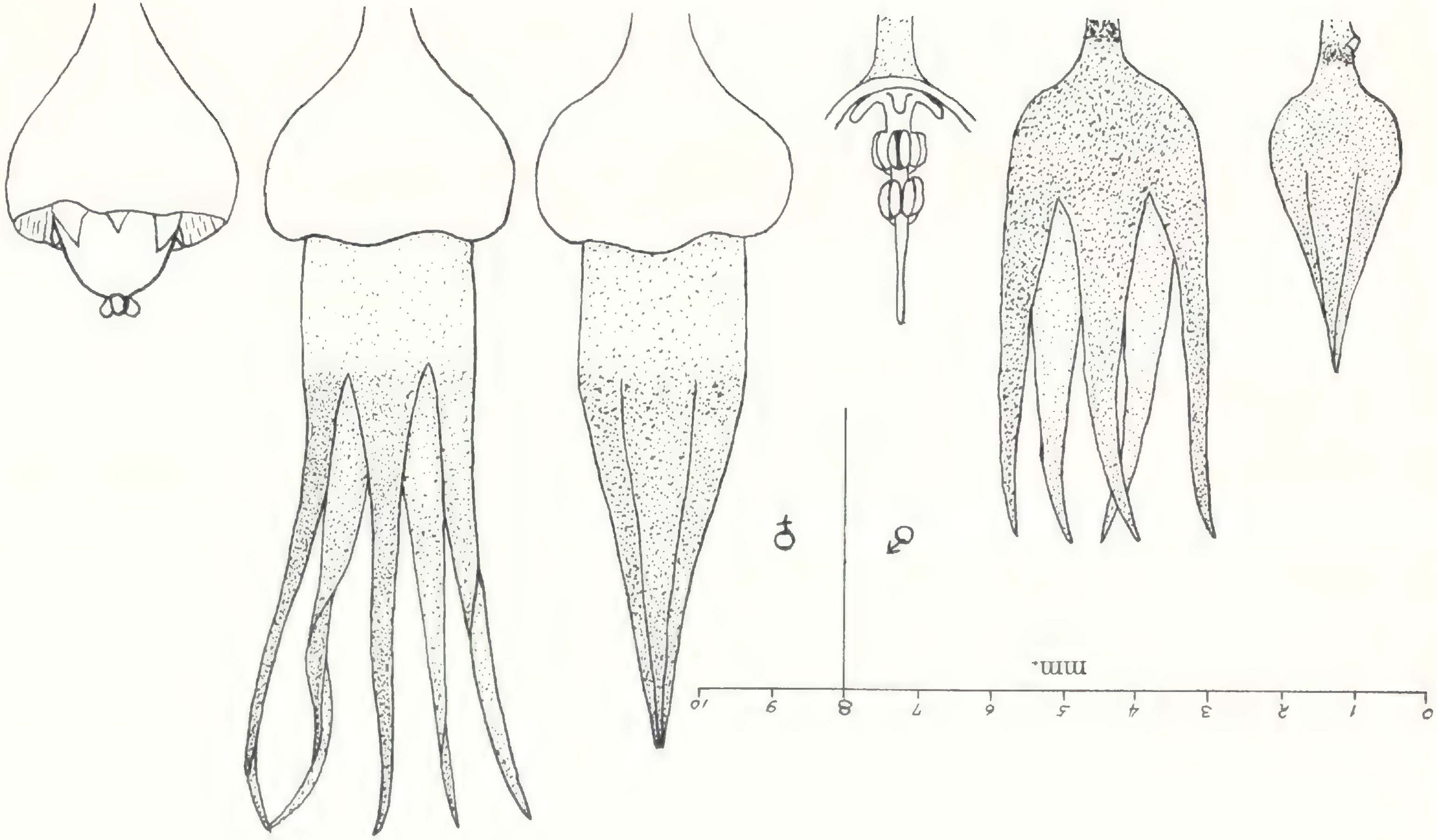
EXPLANATION OF PLATE

PLATE 39

Hevea microphylla. Staminate bud, open and dissected flowers; pistillate bud, open and dissected flowers.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Explanation of Plate

PLATE 40

Staminate buds above open flowers of the same species.

Fig. 1. *H. guianensis.*

Fig. 2. *H. Spruceana.*

Fig. 3. *H. pauciflora.*

Fig. 4. *H. nitida.*

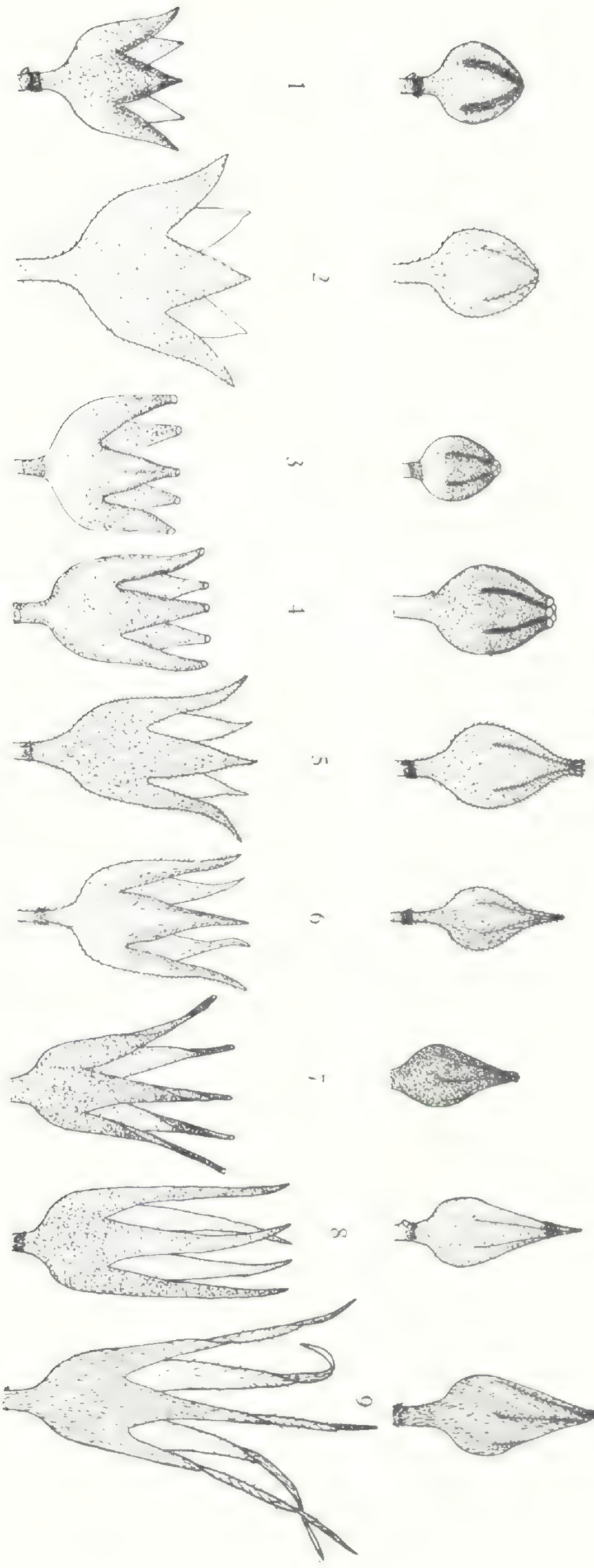
Fig. 5. *H. guianensis* var. *lutea.*

Fig. 6. *H. Benthamiana.*

Fig. 7. *H. brasiliensis.*

Fig. 8. *H. microphylla.*

Fig. 9. *H. rigidifolia.*



SEIBERT—HEVEA IN PERU

Explanation of Plate

PLATE 41

Pistillate buds above open flowers of the same species.

Fig. 1. *H. guianensis.*

Fig. 2. *H. Spruceana.*

Fig. 3. *H. pauciflora*

Fig. 4. *H. nitida.*

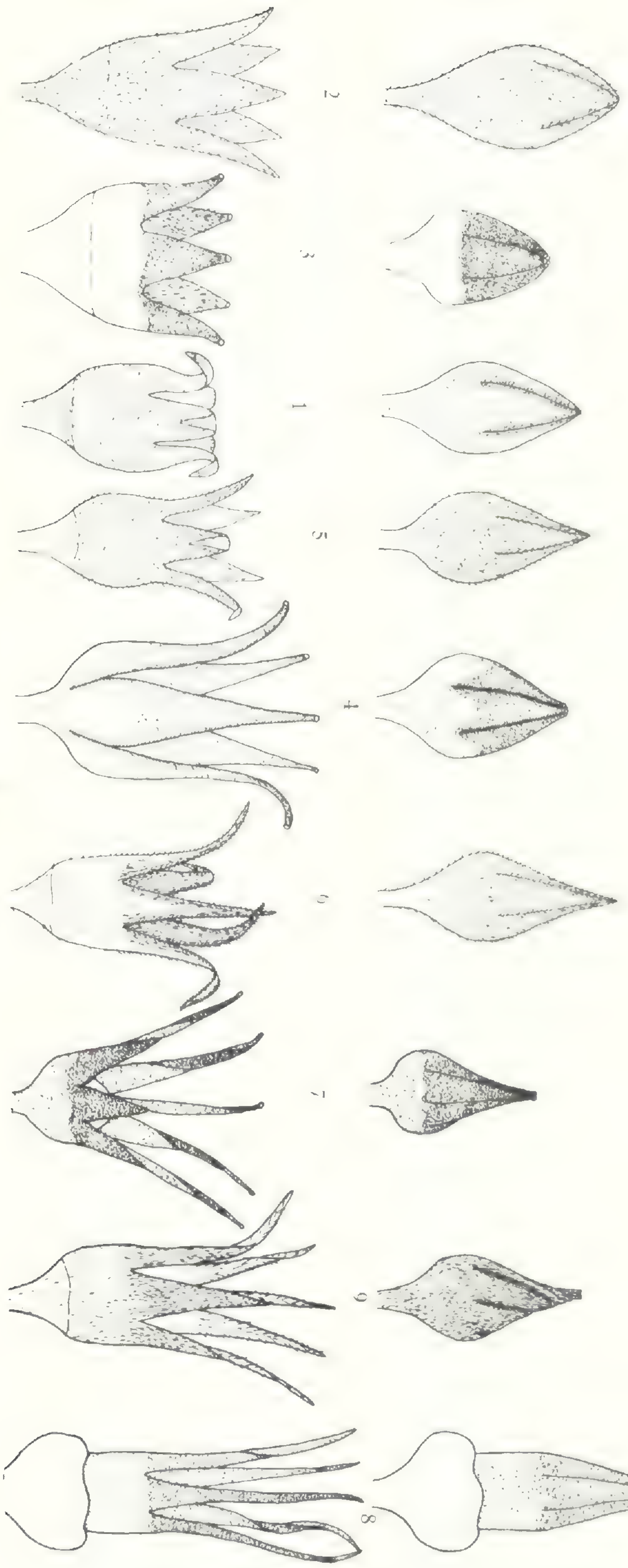
Fig. 5. *H. guianensis* var. *lutea.*

Fig. 6. *H. Benthamiana.*

Fig. 7. *H. brasiliensis.*

Fig. 8. *H. microphylla.*

Fig. 9. *H. rigidifolia.*



SEIBERT—HEVEA IN PERU

Explanation of Plate

PLATE 42

Male reproductive organs above female organs of the same species.

Fig. 1. *H. guianensis.*

Fig. 2. *H. Spruceana.*

Fig. 3. *H. pauciflora*

Fig. 4. *H. nitida.*

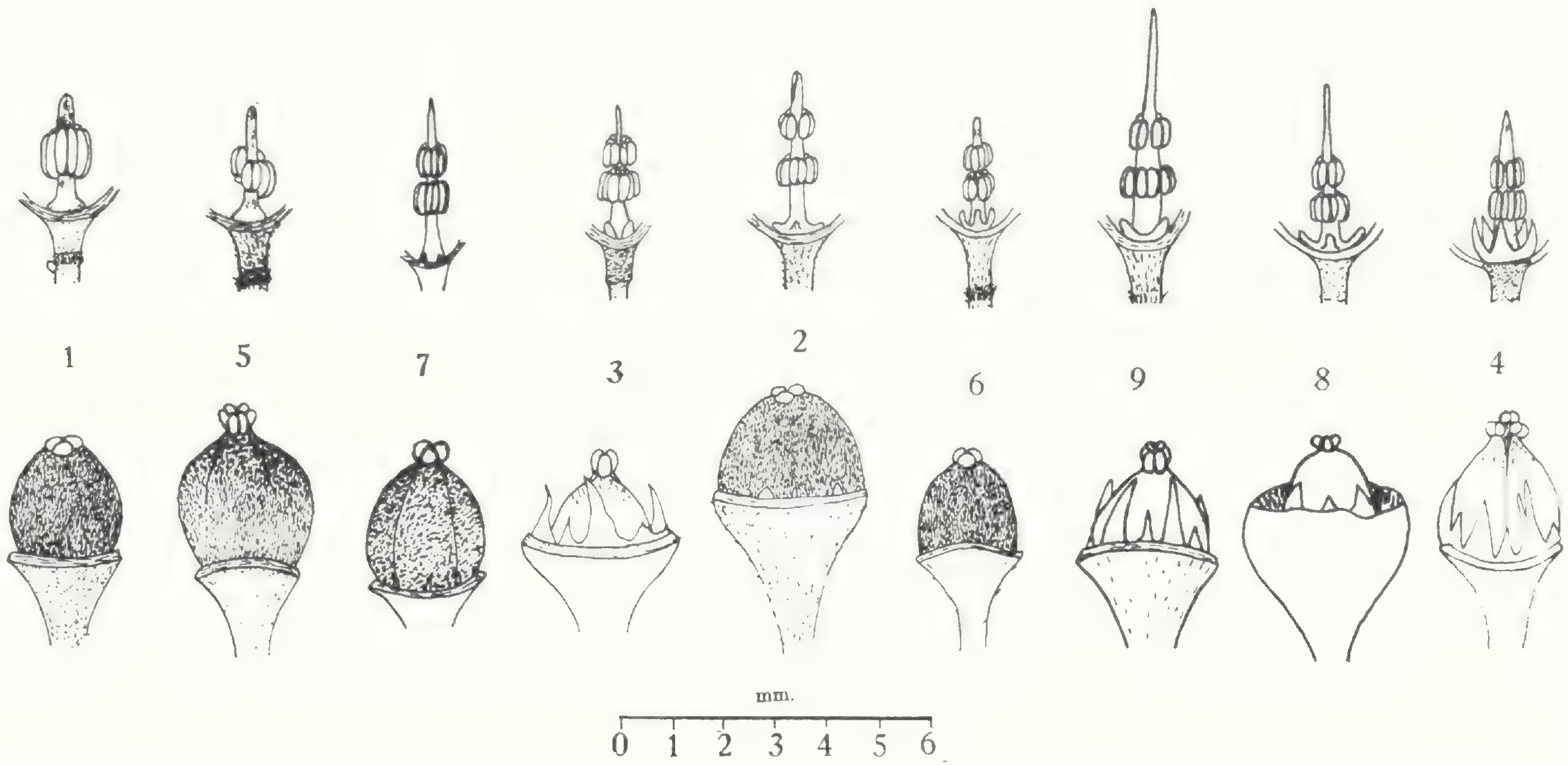
Fig. 5. *H. guianensis* var. *lutea.*

Fig. 6. *H. Benthamiana.*

Fig. 7. *H. brasiliensis.*

Fig. 8. *H. microphylla.*

Fig. 9. *H. rigidifolia.*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Explanation of Plate

PLATE 43

Fig. 1. *Hevea nitida.* Terminal portion of two panicles, showing the terminal pistillate flower with calyx lobes and after calyx-lobe abscission. Note disk lobes at base of ovary. Staminate flowers conspicuously show the calloused calyx lobe tips. Scale in millimeters.

Fig. 2. *Hevea microphylla.* Terminal portion of two panicles, showing the terminal pistillate flower with calyx lobes and after calyx-lobe abscission. Note the conspicuous torus development in this species. Both the staminate and pistillate flowers show the acutely acuminate calyx lobes which are not calloused. Scale in millimeters.

Fig. 3. *Hevea rigidifolia.* Portions of panicles, showing contortion of the bud tips. Scale in millimeters.

1

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SEIBERT—HEVEA IN PERU

Explanation of Plate

PLATE 44

Changes of natural habitat on outskirts of Iquitos, Peru, made by man through clearing and pasturing. Hybrid swarms of *H. brasiliensis* × *pauciflora* and *H. guianensis* var. *lutea* × *pauciflora* occur in this type of habitat, representatives of which are shown.—Photos by Dr. Richard Evans Schultes.

SEIBERT—HEVEA IN PERU

Asclepias tuberosa cl. *tuberosa-interior*

Annals
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SOME DYNAMICS OF LEAF VARIATION IN *ASCLEPIAS TUBEROSA*

ROBERT E. WOODSON, JR.

I. Introduction

One day many years ago, as a young student, I paid my first visit to the Smithsonian Institution in Washington. When noontime arrived, I was taken in tow by my new friend, E. P. Killip, to the Smithsonian's unofficial "Lunch Mess" in the kitchen of an old house around the corner. There I was awed by my inclusion within a jovial group of biologists previously known to me only by their eminence. Killip announced me as a budding authority on the Asclepiadales, an order of Flowering Plants including the milkweed genus, *Asclepias*. Instantly the late Dr. F. V. Coville fixed me with a baleful glare and thundered: "All right, then tell us what is wrong with *Asclepias tuberosa!*" I was dumb-struck. I knew *A. tuberosa* in the field about my home in St. Louis, but it had never occurred to me that anything was "wrong" with it; and besides, I was having troubles of my own with my dissertation topic, the exasperating genus *Apocynum*.

At any rate, when my taxonomic studies finally brought me to *Asclepias* shortly before the outbreak of the recent World War, I already was prepared to find something "wrong" with *A. tuberosa*. And I did. The species, as is usual in the genus, is beautifully distinguished by sharply defined floral and vegetative characters; it is easily keyed from its congeners. But within the species extraordinary variation is rampant, particularly in the leaves. By overworking my taxonomic intuition, at length I was able to distinguish three subspecies, which went far toward resolving the difficulty. But I could not escape the knowledge that something still was "wrong," particularly at the peripheries and commissures of the subspecific distributions. Nevertheless, but for the outbreak of the war I probably would have been content to let well enough suffice.

Every taxonomist is all too familiar with the professional handicaps imposed by a world conflict. Even for those who fortunately are left at home, special duties demand attention. Furthermore, necessary facilities for research are cur-

tailed, such as the exchange of authentic or type specimens. Nor can one overlook the difficulties of publication itself, thanks to wartime industrial disturbances. Anticipating this prospect, I decided to take advantage of international catastrophe by familiarizing myself with some of the more recent tools of biological systematics to the end of applying them to the special problems presented by *Asclepias tuberosa*.

II. Biology of the Species

Asclepias tuberosa is familiar to practically any one who is interested in wild flowers from Sonora to Massachusetts and from Minnesota to Florida. Throughout approximately the eastern half of the United States it is a common roadside plant, conspicuous to any passer-by because of its clusters of stems about knee-high, each surmouted in midsummer by showy trusses of smallish but intensely brilliant orange, scarlet, or yellow flowers. The plants are long-lived perennials of easy culture, and are prized by many horticulturists because of their dependability, long season of bloom, and dramatic dashes of color.

Not the least interesting feature of the flowers is their apparently irresistible appeal to insects, particularly Hymenoptera, which are their chief pollinating agents. Butterflies, as well, are almost constantly hovering above blooming plants, and are responsible for their most familiar popular name of butterflyweed. Coralweed also is an appropriate name for them. Fortunately less familiar are the names pleurisyroot and chiggerweed.

VEGETATIVE HABIT

A fully developed butterflyweed usually is a rather massive plant. The perennial portion consists of a woody tap root as much as three feet long and eight inches in circumference, surmounted just below ground level by a tightly branching crown from which a few to as many as a hundred herbaceous flowering stems may arise each year. Plants attain blooming age two to three years after germination of the seed and may persist for as long as twenty years or more. It would be difficult to estimate the age of a large plant upon a single examination because of the numerous stems produced each season and their crowding at the crown.

Some botanists would refer to the perennial plant body which has just been described as a "clon," and the term has been applied to the essentially similar structure in the Viorna section of *Clematis* (Erickson, 1945). It should be borne in mind that in butterflyweeds, as in other similar plants, the communities of clustered stems have no greater degree of individuality than have the separate twigs of a tree. They are connected organically to the same tap root, and are ramifications of a single embryonic plumule. In butterflyweeds there are no vegetatively reproducing stolons, rhizomes, gemmiferous roots, nor other special propagulae. It is conceivable that accidental or purposeful operation might result in the successful division of the crown into two or more parts, although I have not been successful in the attempt. But such division in nature, if it occurs at all,

must be contrary to the habit of the species, since I have observed no instance amongst the several thousand living plants which I have examined.

It so happens that in certain other species of *Asclepias*, as in the common *A. syriaca*, adventitious buds upon special gemmiferous roots habitually succeed in multiplying single plants. These compose true clons such as those of *Hemerocallis*, *Iris*, *Robinia*, and other spontaneously vegetative-propagating plants. To call the plant of butterflyweed a clon in my opinion not only is misleading but destroys the contrast of the vegetative propagation of such a species as *A. syriaca*. It is difficult to imagine a plant which under some unusual circumstance might not become divided into two or more. If a term is allowed to become a quibble, its significance is lost.

The herbaceous stems of butterflyweed range approximately from one to three feet in height. They normally are unbranched save at the terminal region of inflorescence, although occasional axillary branches may be encountered most frequently as the traumatic result of early decapitation. It must be emphasized at this point that the herbaceous stems are produced at one time at the beginning of each season, and are of essentially identical age. They are remarkably similar in height and rate of development, as well as in number and relative size of parts. These factors are of obvious advantage in the random collection of leaves for statistical analysis.

The stems of butterflyweed are determinate, ending in an umbelliform cyme of approximately one to two dozen pedicellate flowers. In most fully developed plants the terminal cyme is subtended by two or more leafy-bracted, scorpioid branches studded at the nodes with umbelliform cymules developing in acropetal succession. These branches obviously are the homologues of the branches of a dichasium. The determinate inflorescence character of *A. tuberosa* is an anomaly amongst the American species of *Asclepias*. It is an extremely fortunate one from the standpoint of these investigations, since it further facilitates the collection of leaves of nearly identical physiological age, which would be a precarious operation upon an indeterminate axis.

The leaves are simple, entire, and are irregularly alternate or spirally arranged. The number, shape, and size of leaves are extremely important characters in the distinction of the subspecies, and will be discussed in later paragraphs of this section. Obviously, the leaf variability is such that it forms the subject matter for these investigations.

REPRODUCTIVE HABIT

The flowers of *Asclepias* are classical examples of entomophily and are equalled in complexity only by those of the orchids. In the present connection it will probably suffice to recall only those features immediately concerning pollination and the production of seed. In the center of a butterflyweed flower, as in other milkweeds, there arise five cornucopia-shaped bodies which are petalaceous, and are in fact often mistaken for the corolla. These are the *hoods*, the nectar-secreting

bodies which are the goal of the insect visitors. The hoods actually are outgrowths of the staminal filaments, the smaller anthers of which they virtually conceal.

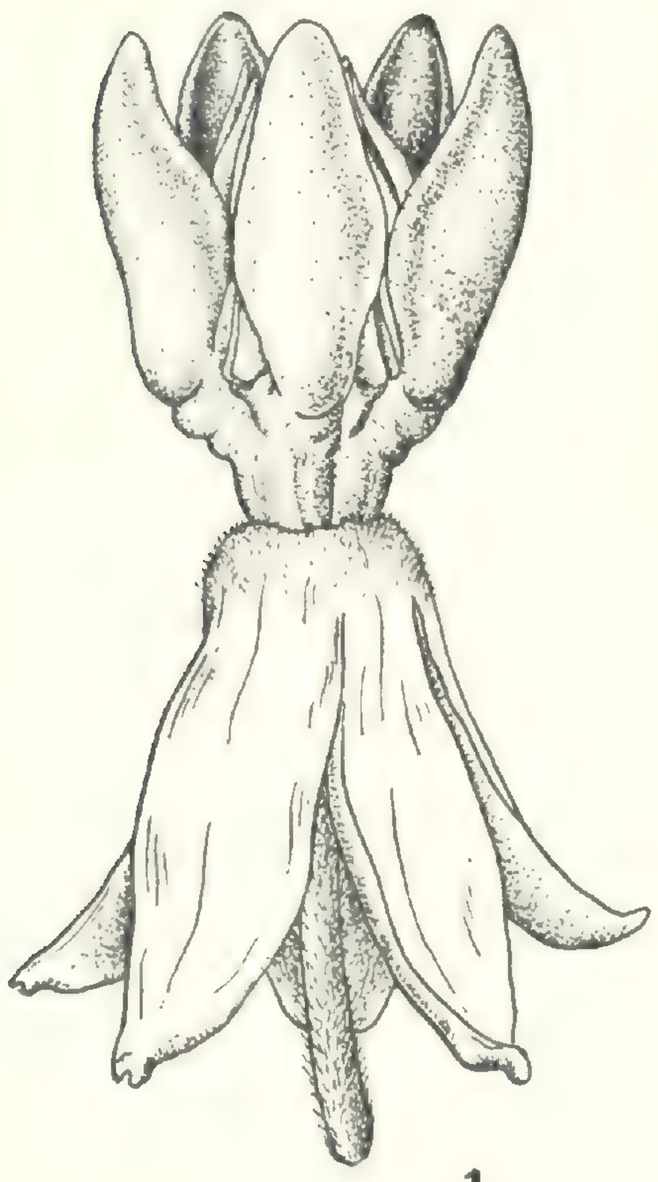
The anthers themselves are closely connivent in the form of a cylinder or truncated cone about the stigma. Each anther contains two pollen cavities. A remarkable feature of milkweed pollen is that it is borne within small, flat bags, or *pollinia*, the confining membrane being derived from the tapetum. Still more remarkable is the fact that the pollinia of adjacent anthers are joined together in pairs by means of a delicate yoke-apparatus *(translator)* surmounted by a pad-lock-shaped body known as the *corpusculum*.

The corpusculum bears upon its outer face a more or less conspicuous cleft. It is well known that pollination is initiated when a strong insect, such as a wasp, accidentally thrusts its barbed legs between the anthers while scrambling about the center of the flower in search of nectar. If a barb of the insect's leg wedges into the cleft of the corpusculum, a stout pull of the member usually succeeds in withdrawing the pair of pollinia from the anthers. It is a common sight to see wasps or bees flying about a blooming butterflyweed, their legs laden with pollinia.

Robertson (1892) has enumerated 15 species of Lepidoptera, Hymenoptera, and Diptera collected while bearing on their bodies pollinia of *Asclepias tuberosa* in the neighborhood of Carlinville, Illinois. Amongst these is *Apis mellifera*, the common honey bee, which is known to have a flight radius of one-half rarely to five miles. It is difficult to secure data concerning the radius of flight of the other possible pollinators, although the phenomenal migrations, some hundreds of miles, of certain Lepidoptera are well known.

I do not wish to over-emphasize the efficacy of the floral mechanism of *Asclepias* with regard to insect visits, since it does not appear to be very high. Certainly less than 1 per cent of the flowers normally set fruit, except in *A. incarnata*, the swamp milkweed, in which sets may amount to 25 per cent. An additional factor to recall, in connection with insects as pollinators of *Asclepias*, is that the pollinia appear to be highly irritating to the carrier. On several occasions I have trapped wasps of the genus *Chlorion* in transparent bags, when they invariably appear to be more anxious to divest themselves of the pollinia than to escape.

The stigma of the milkweed flower is surrounded by the connivent anthers and is a rather complex structure. The receptive surface is not at the flat top, but actually is divided into five concave surfaces which alternate with the anthers and are closely protected by them. In order that a stigmatic surface be pollinated, it is necessary to introduce a pollinium between the flanged, cartilaginous, marginal wings of the anthers, an extremely delicate and nerve-wracking operation for a human experimenter. That the feat is accomplished at all by the chance movements of an insect seems nothing short of marvellous, and that so few fruits usually are observed upon a single plant is quite understandable.



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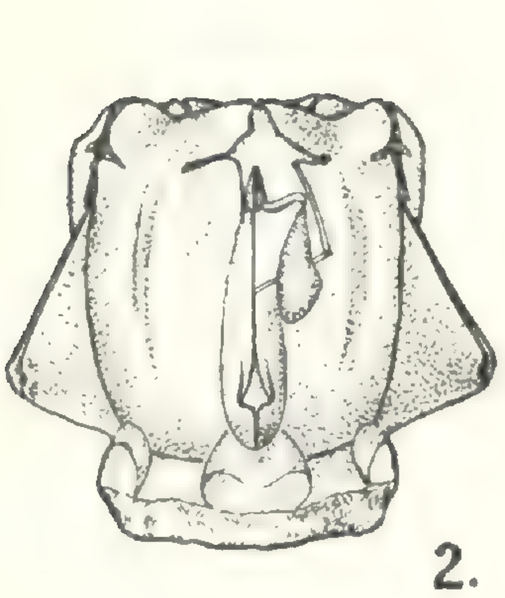

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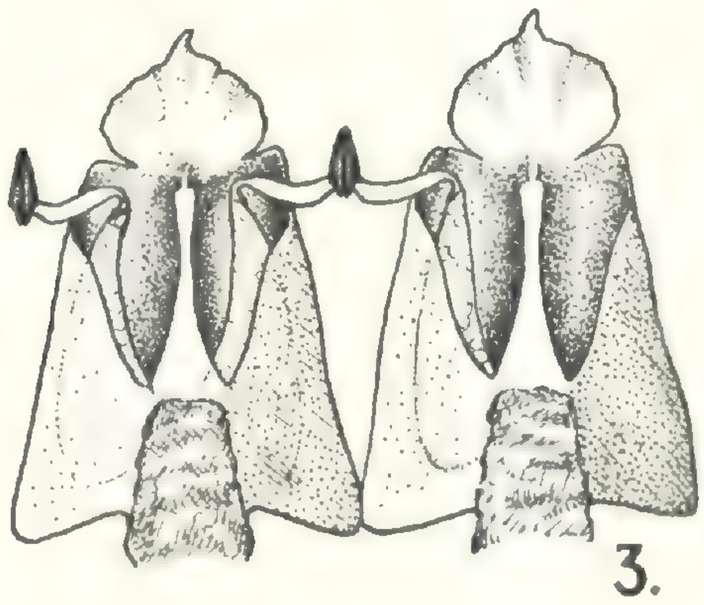

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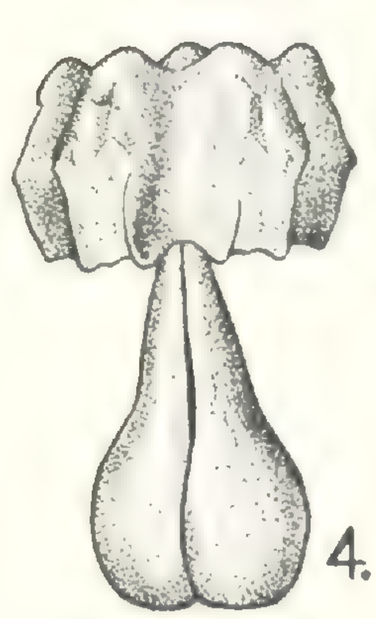

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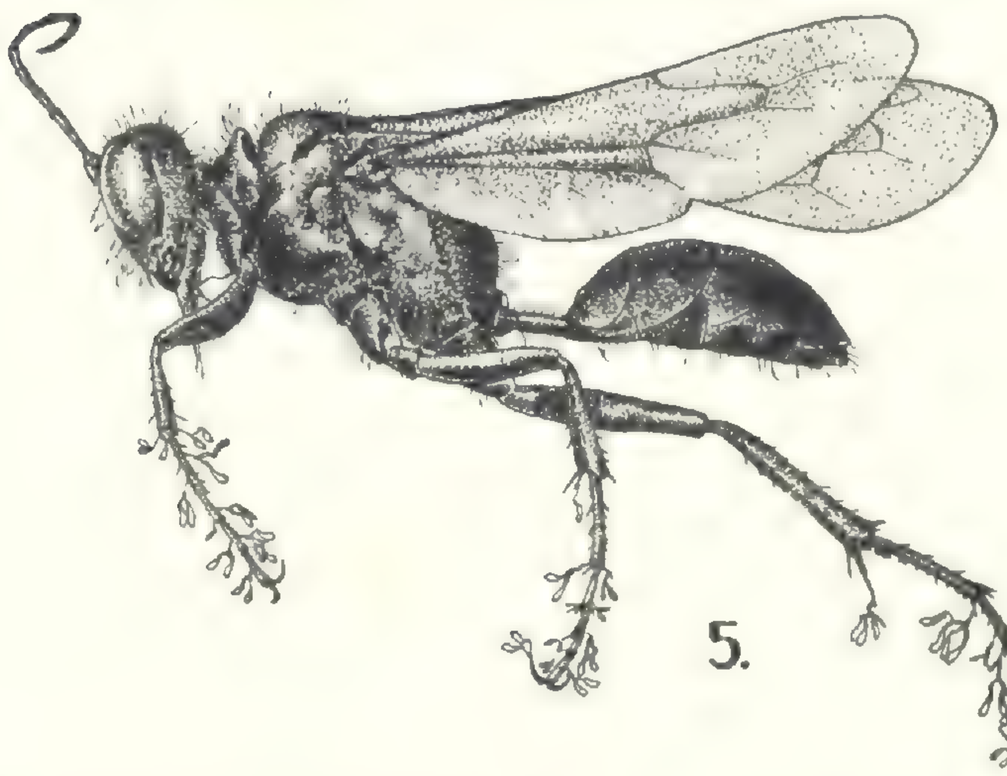

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E Herbold Froeschner

Reproductive mechanism of *Asclepias tuberosa:* 1, flower; 2, gynostegium with hoods removed, showing connivent anthers with one pollinium protruding; 3, two anthers as seen from within, showing pollinia; 4, carpels with stigma head, showing two stigmatic surfaces; 5, *Chlorion* sp. bearing pollinia on feet; 6, pollinia enlarged, attached to barb of insect's foot; 7, follicles with comose seeds.

Size and shape of pollinia, corpuscula, anther wings, and stigmatic chambers vary greatly amongst the species of *Asclepias*. Hense it is not surprising that interspecific hybridization within the genus is very infrequent. After over a decade spent in studying it, I doubt whether I have observed many more than a dozen instances of putative hybrids amongst the approximately 80 species.

The only record of a successful experimental cross between distinct species is that of *A. speciosa* × *syriaca*, first performed by Stevens (1945). In crosses involving other species, Moore (1946a) occasionally observed preliminary swelling of the ovary, followed by abortion. This he interprets as due to somatoplastic sterility. Although successful self-pollinations have been reported by several authors for certain species of *Asclepias* (notably Stevens, 1945), similar experiments by Moore (1946b) were unsuccessful. My friend F. K. Sparrow has told me that his extensive pollinations with *A. syriaca* reveal clonal self-sterility. My

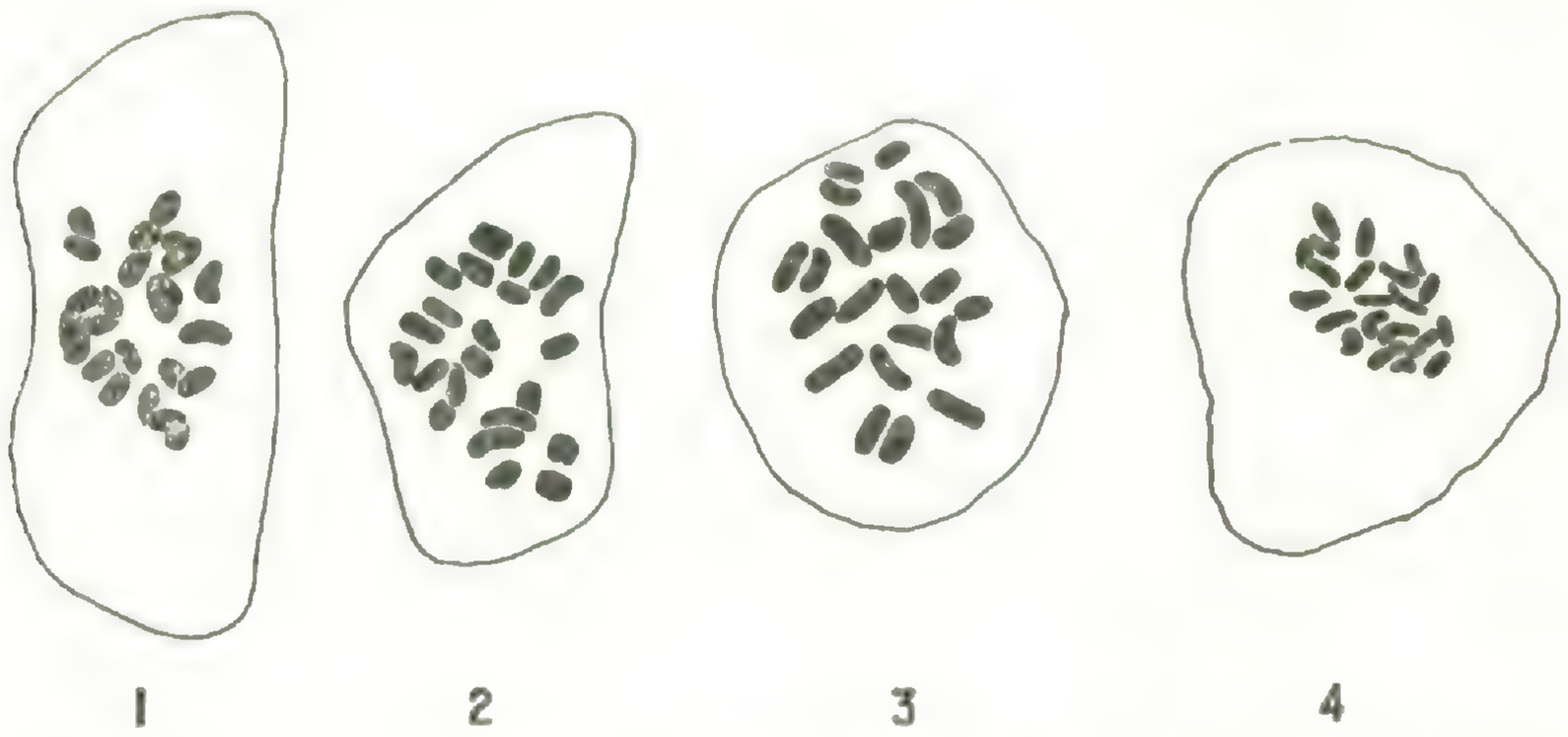


Fig. 1. Somatic metaphases from young leaves of *Asclepias tuberosa* in different parts of its distribution: 1, Stillwater, Okla.; 2, Glendale, Mo.; 3, Westport, Conn.; 4, Snail Lake, Minn.—All figures × 1500.

own limited experiments at self- and cross-pollinations involving *A. tuberosa* have been notably futile. I suspect that special mechanical factors may account for the difficulty in milkweed pollinations, such as the degree of desiccation of the tapetal membrane, which must split to allow the emission of the pollen tubes.

The fruit of butterflyweed consists of solitary, or infrequently paired, narrow, fusiform follicles up to 15 cm. in length. Upon dehiscence as many as 100 compressed, oval seeds approximately 0.4 cm. long are released, each provided with the micropylar parachute of silky hairs so diligently studied and collected as a substitute for kapok during the recent war. The silky parachute, technically called the *coma*, is extremely bouyant, and is doubtless capable of conveying the attached seeds for long distances, even approximate estimates of which, however, are unavailable.

I have found during the course of progeny tests that viability of the seeds is fairly high as a rule, but that germination is very irregular, proceeding in some samples for well over a month. Although I am not yet ready to publish con-

clusions upon these tests, they indicate at the present writing that the various leaf modifications encountered in different parts of the species' distribution have a genetic basis and are maintained within sufficient limits under cultivation in my test plots.

CYTOGENETICS

Chromosome counts for *Asclepias tuberosa* made by various workers, notably Moore (1946), agree in the figure $n = 11$. This is also the base number for all other Asclepiadaceae investigated. Polyploidy has not been reported in *Asclepias*, although tetraploids occur in certain other genera, particularly in the Orient. Somatic metaphases from young leaves of *A. tuberosa* in various parts of its range are reproduced in fig. 1. The chromosomes are small (about 2 μ long) and relatively uniform, and are poor subjects for configuration or structural studies.

ECOLOGY

In its geographical distribution from southern peninsular Florida to northern Sonora and from the Ottawa River to the Black Hills of South Dakota, *Asclepias tuberosa* demonstrates its wide climatic adaptability (Map I). It is clear from the map, as well as substantiated by my field observations, that the species is best adjusted to its environment in the mesothermal and southern microthermal climatic regions of North America. Where it is found in the western steppe climates it is probably as a scattered relic of former mesophytic times.

Something of the climatic preferences of butterflyweed can be deduced from a comparison of the distribution map of the species with standard climatic charts of North America. At least in general outline, it appears that the July mean temperature is critical in relation to density of population of the plants, a normal mean surface temperature of 68° to 86° F. indicating roughly the optimal limits. Precipitation appears to be more critical than temperature, however, suggesting general requirements of an annual mean of over 20 inches. It is very striking, when traveling eastward across Kansas in midsummer, to find the butterflyweed suddenly emerge from more sheltered positions as a common roadside plant on the outskirts of Topeka, near the boundary of the tall-grass prairies and the short-grass plains.

In the opinion of some, *Asclepias tuberosa* should be considered as a prairie type, or even as an emigrant from the dry plains or deserts of northern Mexico. To my mind it accords more closely with the facts of distribution to regard it as indigenous to the glades and open woodlands of the southern hardwood forests, from which it has spread to the southeastern longleaf, loblolly, and slash pine forests, and to the southwestern pinyon-juniper-yellow pine woodlands. When one considers that approximately the northeastern third of the species' present distribution has been available for plant colonization only since the Pleistocene, it is clear that establishment of populations is taking place to the northeast much more rapidly than to the southwest.

Butterflyweed is found at elevations from near sea-level to about 6000 feet altitude. In the western states progressive desiccation of the plains appears virtually upon the point of eliminating the species except upon the well-watered highlands. In the plains the plant must seek the protection of ravines and canyons, or larger neighboring plants.

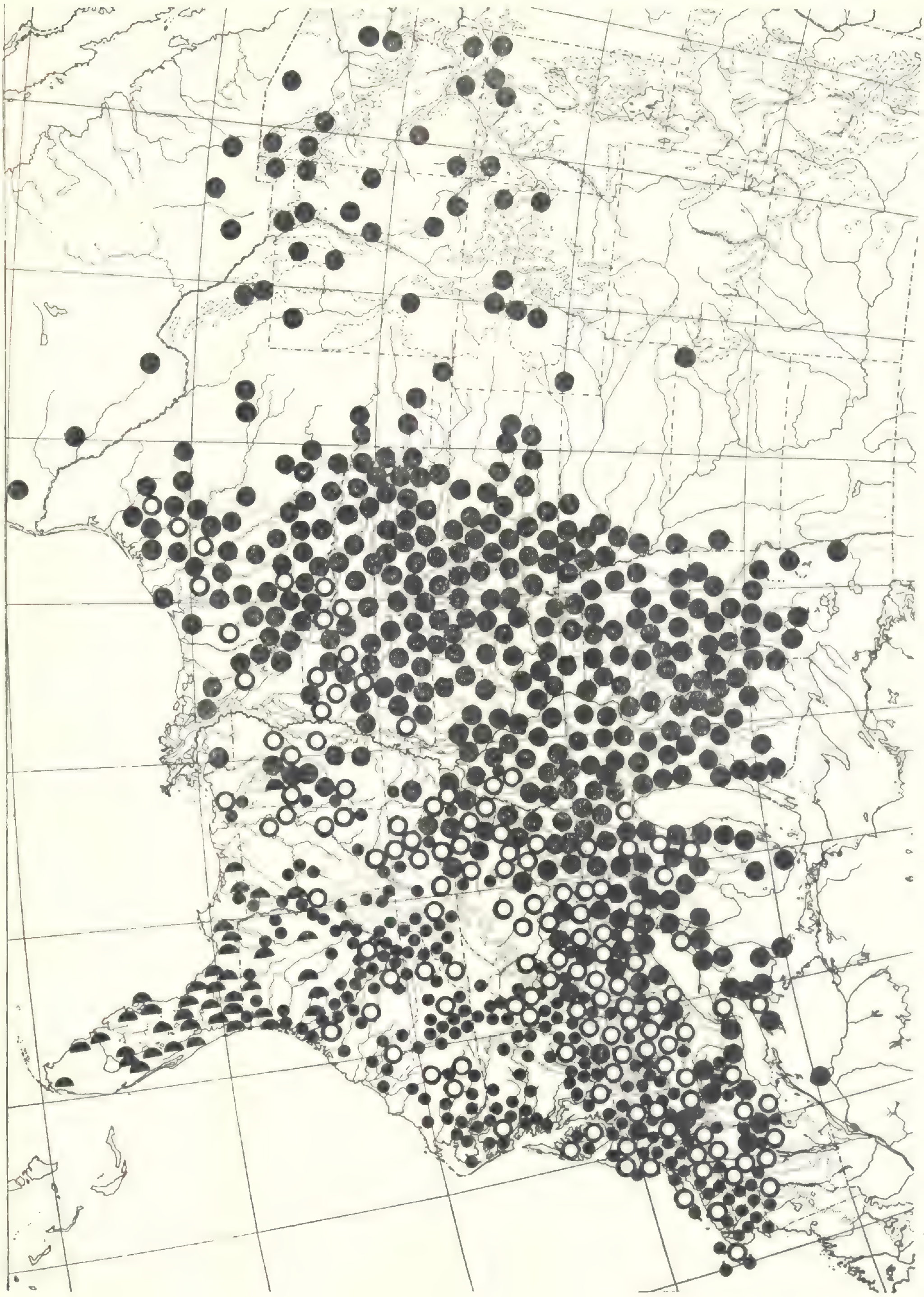
The wide distribution of *A. tuberosa* bespeaks its tolerance for a broad range of edaphic conditions. Horticulturists are in the habit of prescribing for it a sandy soil, upon which it undoubtedly flourishes, but scarcely more so than upon the exceptionally tight clays known as "crawfish soil." Although I have made no attempt to determine its pH preferences, they probably are circumneutral since I have found fine colonies of plants growing impartially upon dolomitic limestone, argillaceous shale, and granitic detritis. An unusually large colony was found on an alkaline flat in western Texas, but the plants appeared depauperate. Good soil drainage appears essential for optimal growth, and a "poor" soil is generally preferable to a "rich" one. I do not remember ever having found it growing on alluvium.

Butterflyweed is found occasionally as single plants, but more frequently in colonies of three or four to well over a hundred individuals. Distance between colonies varies notably with respect to local climatic and vegetational conditions. Roughly east of the 96th meridian the species is a common roadside plant, as has been discussed before. Through eastern Kansas and Missouri the colonies may be encountered at intervals averaging about ten miles apart.

Through the prairies of south-central Illinois, on the other hand, I was able to find only three colonies along the route of about 150 miles between St. Louis and the Wabash River. From southern Indiana to West Virginia the colonies become somewhat more frequent, and reach their greatest frequency, somewhat more than in Missouri, from West Virginia to the coast of Virginia. The brief account of this transect summarizes observations made during a collecting trip in the summer of 1946. Statistical details will be presented in a subsequent chapter.

Roughly west of the 96th meridian butterflyweed is scarcely ever encountered along roadsides through the Great Plains. The plants are found, if at all, only along the infrequent water courses, particularly at the heads of ravines. The size of colonies is considerably smaller than is customary in the East, and the distances between them is far greater. It is only in the pinyon-juniper-yellow pine highlands of the southwestern states that butterflyweed again becomes a fairly frequent plant.

I believe that colonies usually develop from seedlings of a single parent plant. This is indicated not only by their considerable degree of isolation, but by the centering of leaf variation amongst individual plants about more or less distinctive colonial means for the various characters measured.



Map I. Distribution of *Asclepias tuberosa*: each symbol represents a single county record. Large dots: *A. t. interior*; small dots: *A. t. tuberosa*; hollow circles: putative hybrids *A. t. tuberosa* × *interior*; half-circles: *A. t. Rolfsii*.

THE THREE SUBSPECIES

Ordinary herbarium methods disclosed at the outset of these investigations the presence of three subspecies of *Asclepias tuberosa* (Woodson, 1944): *A. t. tuberosa*, with leaves typically obovate to linear-oblanceolate, the base usually cuneate or rounded; *A. t. interior*, with leaves typically ovate to ovate-lanceolate, usually with cordate or truncate base; and *A. t. Rolfsii*, with leaves essentially as in ssp. *tuberosa* but predominantly with more or less conspicuous hastate or cordate dilation toward the base and with the margins more or less crisped. Map I shows the known distribution of the three subspecies and indicates the probability that the centers of modern dispersal, if not of actual origin, may be regarded as the Paleozoic land masses Appalachia and Ozarkia, and the early Mezozoic "Orange Island," now north-central Florida, respectively.

It is difficult to indicate with such a map the variation and intergradation of taxonomic units, since in this case only three types of symbol are employed. In addition to the symbols for the separate subspecies, however, a fourth, the hollow circle, has been introduced to indicate intergradations of *A. t. tuberosa* and *A. t. interior*. A fifth type of symbol might further be used to show intergradation of *A. t. Rolfsii*, particularly with ssp. *tuberosa*, since as it stands the map rather implies that *Rolfsii* is genetically more isolated than the other two subspecies.

As a matter of fact, such is far from being true. The distribution of hollow circles suggests that in southern Alabama and southern Georgia one might expect to find intergradations of all three subspecies. This actually appears to be the case, and the practical limits of such a map stand revealed. A fifth symbol is not used for intergradations of *Rolfsii* simply because I cannot distinguish the separate roles of the three subspecies satisfactorily.

Almost the first glance at Map I will show that although ssp. *tuberosa*, indicated by small dots, is distributed roughly from the western Appalachian foreland to the coast, with *interior*, indicated by large dots, to the west and north, the hollow circles, which indicate subspecific intergrades, extend from the commissure of the subspecies completely through the distribution of ssp. *tuberosa*. It is clear even from routine examination of herbarium specimens that *tuberosa*, situated unstrategically between *interior* and the sea, is in the process of genetic dissolution.

This situation appeared so interesting that a biometric study of natural and artificial populations of *A. tuberosa* was begun early in 1942. Begun as a side-line to my more orthodox systematic studies, my hobby soon grew to occupy the majority of my research. So many additional topics of interest arise as time passes, and so many new lines of attack suggest themselves, that the study might possibly be continued as long, if scarcely so profitably, as the classic investigations of Sumner on *Peromyscus*.

III. Exploratory Methods

The disadvantages of the type of distribution map which has just been presented in the previous chapter are the simple consequence of the use of a discontinuous scale with too few intervals. Nevertheless I do not wish to minimize its use. In dealing with a genus of many species, such as *Asclepias*, it is ordinarily the only type practicable. It at least states the known range of one or more taxonomic units and perhaps suggests the region of any intergradation. To an imaginative mind one of its virtues may be that it asks more questions than it answers.

When a continuous scale is available, however, measurements of a large series of specimens may allow the accumulation of equally spaced means and their accompanying measures of variability, and the result is a "phenocontour map" such as that advocated by Huxley (1938). As yet few phenocontour maps have been published. Possibly the most familiar examples are those of Alpatov (1929) for *Apis mellifera*, the common honey bee, in European Russia. These, in my opinion, suffer chiefly because of the relatively few and irregularly distributed localities into which the many samples fall. A better instance is provided by Pearson's (1938) geographic study of melanism in the Tasmanian bush opossum, *Trichosurus vulpecula fuliginosus*, in which definite contour lines ("isophenes") were obtained. In a class by itself is the world chart of human blood groups presented by Boyd (1939).

From a phenocontour map benefits may accrue from several directions. The biogeographer may plot with a degree of mathematical precision the migrations and environmental adjustments of which he now speaks in more general terms. The cytogeneticist may be given wholesale data of population dynamics upon which to apply a gamut of attractive theory much of which still requires exemplification. Last, but not least, opportunity finally is given the customarily inarticulate systematist to prove the detail of his observations to a disbelieving world. The inexorable accumulation of specimens to catalogue for the benefit of others may allow but one such opportunity, and it should be taken.

USE OF THE HERBARIUM FOR POPULATION STUDIES

There can be little doubt that systematic botany has contributed far less to recent advances in the study of evolution than has systematic zoology, and one reason for this has been its neglect of modern statistical methods. Yet for ready collection of data, ease of manipulation, and wealth of museum material, plants in general are much more favorable subjects for study than are animals. No one has appreciated these advantages more than did Charles Darwin, who bequeathed a part of his estate for the founding of the 'Index Kewensis,' the herbarium taxonomist's most indispensable single tool.

Herbarium specimens are not a perfect substitute for living plants, but they offer incalculable advantages for the interpretation of field studies. Not all plant materials are adequately preserved by the usual herbarium methods of press-

ing and drying, but an astonishing percentage is. In the herbarium of the Missouri Botanical Garden is a collection of several hundred dried plants assembled by one Georg Rudolph Boehmer as material for his 'Florae Lipsiae Indigena,' published in 1750. The appearance of some of these plants is almost as though they had been pressed and dried but a few months ago. All are perfectly recognizable, and we have in them a detailed record of the distribution of plants around Leipsic two centuries ago.

In the early days of botany it was customary to have represented in the herbarium only one or two specimens of each species. Nowadays any of the several major herbaria of the world may include a thousand specimens of a single widespread species from all parts of its range, gathered in all stages of its growth at all times of year by faithful collectors, living and dead, for at least a century. When several such collections of a group of plants are united for one's study, the very mass of it is most impressive. The accumulation of material so representative of variation in time and space obviously is beyond the powers of an individual. It is a unique evolutionary heritage.

A false impression widely current among non-taxonomists is to the effect that herbarium specimens usually are collected because of some abnormality which attracts the fancy of the collector. The accusation reveals such prejudice that one is baffled for an effective retort. Perhaps a denial that falls far short of revealing the sincerity of a plant collector but may impress the critical outsider is the fact that plant collections habitually are made in multiplicate sets bearing identical serial numbers for purposes of sale or exchange amongst the numerous botanical institutions of the world. It would be difficult indeed for even an unusually perverse individual to pursue his passion under such adverse circumstances. The chief danger in plant collecting actually is that of choosing too many "normal" specimens. The statistical errors from such likelihood, however, should be ineffective.

"Mass collections," which I prefer to call "local population samples," have been advocated recently by Anderson (1941) and others as an aid to the solution of certain systematic and cytogenetic problems. This method of sampling local variation surely is a very useful one, and a tool which I have used in part in my own work. Certain attendant disadvantages should be discussed, however.

It is known, for example, that the phenotypic responses to the fluctuations of climate may vary from year to year in a given place, as Lewis (1947) recently has shown with respect to *Delphinium*. Population statistics obtained from a given locality for a given year may not be compared safely with samples from other localities at another time, perhaps even during the same year. Employing only local population samples, the task of effectively covering the entire range of a single widespread species, in the case of *Asclepias tuberosa* about 1,500,000 square miles, assumes fantastic proportions.

The most reliable statistics concerning plant populations over a wide area must be made not during a single season but over a span of years, and the samples must be randomly selected and as widely distributed as only generations of differently tempered naturalists can accumulate them. It is possible to meet these requirements only by the use of herbarium collections. It is not a new convenience: plant taxonomists have been enjoying it since long before the birth of Linnaeus.

The advocate of "mass collections" may retort that even though herbarium samples may cover distribution in time and space more effectively, the samples are smaller at best than those specially made by his methods. The statistical fallacy of this argument is obvious. The reader should not infer that I am condemning the use of local population samples. I am merely attempting to point out what I consider to be their limitations and to defend my use of herbarium specimens. I have obtained quite interesting results through using both methods coordinately.

Perhaps this will be an appropriate place to caution firmly against the inconsiderate use of herbarium material for statistical work. Being an herbarium custodian myself I can anticipate the angry protests which will arise from my colleagues at the prospect of their precious charges being plucked, petal by petal, or for that matter, leaf by leaf, by increasing numbers of "biosystematists." We may not treat herbarium specimens as we would living plants having the power of regeneration of lost parts. Type or other authentic specimens must remain sacrosanct for the use of posterity. Only abundant parts of herbarium specimens should be sampled in studies such as these, and then only by an experienced student upon express permission of the proper authority.

Being an herbarium man, my first impulse in beginning my study of leaf variation in *Asclepias tuberosa* was to turn to the herbarium of the Missouri Botanical Garden where I am employed. There I found several hundred sheets of specimens representative of the entire range of the species. Nearly all the sheets I found to bear at least one entire stem of the plant. The leaves of each, habitually numerous, I found to be well preserved, being somewhat leathery in texture. Since they were so abundant, I discovered that at least some had escaped being glued to the paper and could be removed without appreciably damaging the specimen.

After experiment I adopted the procedure of selecting a "random" leaf from about the middle of a single flowering stem of each specimen, if it included more than one stem, and recording the locality (state and county for reasons which will develop) from whence it came. I soon found also that it is desirable to keep a record of the various collectors' numbers in order to avoid statistical bias from measurement of duplicated specimens so prevalent in large herbaria. This entails no unusual inconvenience, being a common monographic practice. The leaves were boiled in water, separately, until completely exhausted of air. Their outlines were then traced upon paper with a sharp 2-H lead drawing pencil, using an illuminated tracing table.

For tracing, I have found best adapted to my needs the large sheets of millimeter grid paper printed by Keuffel & Esser of New York. The 5- and 10-millimeter lines are specially accentuated on this paper, which facilitates both orientation of the tracings and subsequent measurement. The grid paper may be protected from the moistened leaf by placing between them a small piece of wax paper.

To some, I might appear to have been more scientific had I used some photographic means of transferring the leaf outlines. There are several advantages of the tracings, the first of which is the millimeter grid itself, special advantages of which will be indicated. A second advantage is that the tracings can be added to the large grid sheets consecutively as they accumulate, assigning a special sheet to each local population sample, or particular geographic division. In short, the tracings appeared to be more convenient and photographs or blueprints unnecessarily complicated and time-consuming. In measuring smaller objects, greater accuracy doubtless would be obtained by the latter methods. The degree of accuracy obtained through tracing will be discussed presently; I believe that it will be found sufficient for my needs.

QUANTITATIVE MEASURES

It has been explained in previous paragraphs that the chief, if not the only, criteria distinguishing the three subspecies of *A. tuberosa* are found in differences of leaf shape. Size, as measured by median length and width, is of minor taxonomic importance except perhaps in providing abstract universe values. This is usually true because size, although it has a genetic basis, is more directly influenced by environment and age of organism than is shape.

It is easily seen in fig. 2, which consists of very small random samples of leaves, that leaves of ssp. *tuberosa* may be said to be of greatest average width and those of ssp. *interior* of greatest average length, while those of ssp. *Rolfsii* average least in both regards. But an experienced plant systematist probably would prefer to point out that the leaves of *tuberosa* tend to be broadest above the middle (obovate to oblanceolate) with rounded or tapered base, those of *interior* broadest below the middle (lanceolate to ovate-lanceolate), usually with 2-lobed (cordate) base, and those of *Rolfsii* more or less fiddle-shaped (pandurate) and with crisped margins.

Determined to find a suitable continuous scale with which to measure leaf shape in *Asclepias tuberosa,* I finally recognized that the differences in shape, at least those distinguishing ssp. *tuberosa* and ssp. *interior,* resolve themselves into relative differences in width at two points, at approximately one-quarter the median length from the apex and the same distance from the base, respectively. It was obvious that in *tuberosa* the greater width typically is at the upper quarter and in *interior* at the lower quarter. The intergrades usually are found to bear essentially oblong or elliptic leaves, their widths at the upper and lower quarters being approximately equal.

For some time thereafter I measured leaf widths at exactly the upper and the lower quarters of median length, hoping that by the ratios I might be able to distinguish quantitatively the leaves of the two subspecies with respect to unity as represented by the oblong or elliptic leaves of intergrades. This activity ceased when I realized that ratios such as those I was employing are functions of length. Another disillusioning discovery was that both ratios and their reciprocals afford warped scales, and furthermore the warping of the two scales is unequal. I mention these points for the consideration of any who may contemplate using similar ratios in biometric studies.

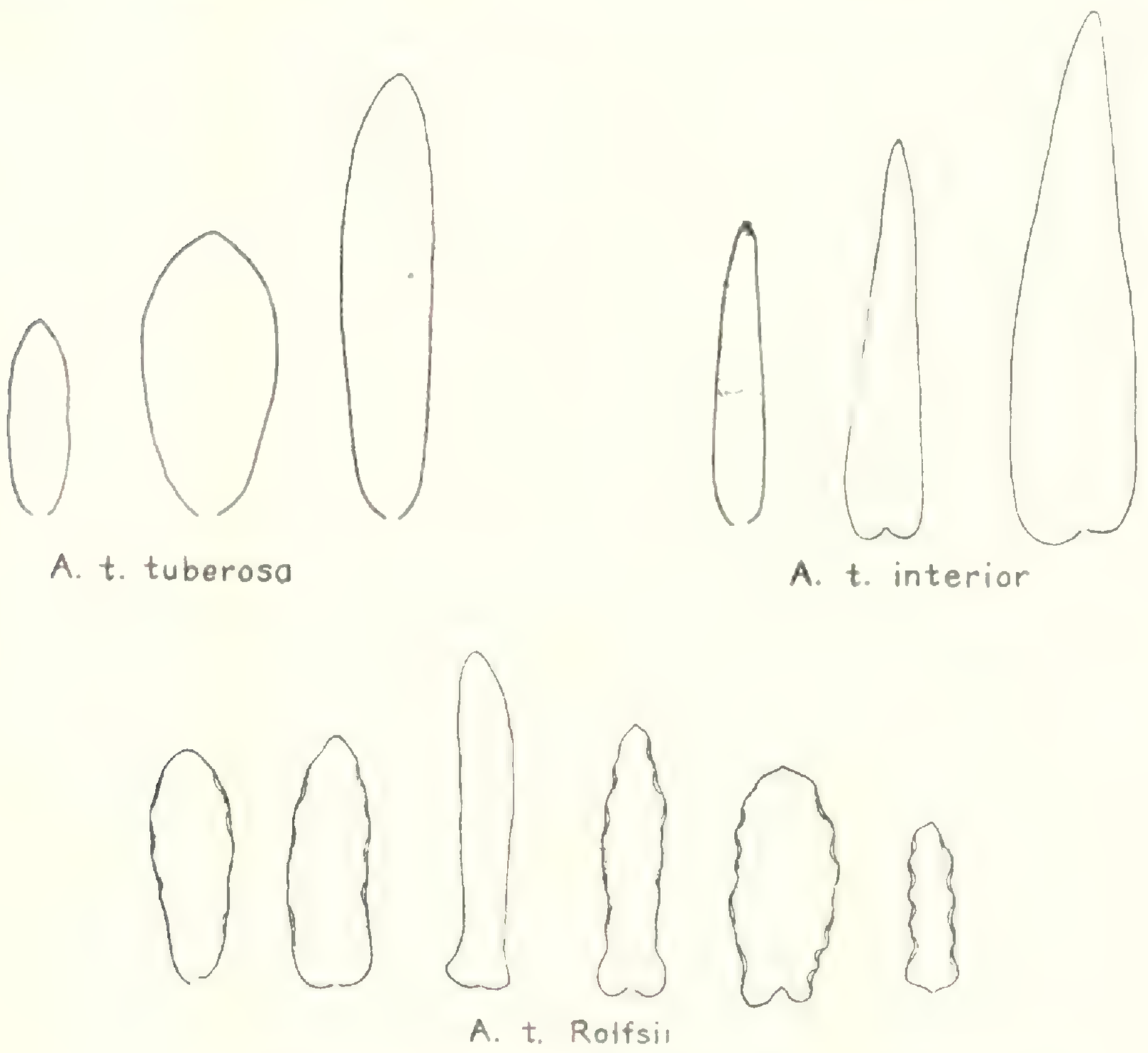


Fig. 2. Representative leaf types of three subspecies of *Asclepias tuberosa*.

The methods which I finally adopted for measuring shape are illustrated in fig. 3. In the diagram to the left of the figure, *AOB* represents the frame by which leaf outlines are oriented at equal distances upon my large grid sheets. The base of the leaf blade, where it joins the petiole, is placed at O and the tip vertically above in the position designated as *B*. After tracing the outline about the frame *AOB*, it is a very easy matter, since 1-, 5-, and 10-mm. distances are indicated on the grid itself, to measure median length to the nearest millimeter as the distance *OB*, rounding to the nearest even figure. Median width, *MM'*, is measured also to the nearest millimeter, at the point midway between *O* and *B*, rounding as

before. It appears unnecessary to read these distances to fractions of a millimeter in the light of what we shall learn concerning the experimental error involved.

It will be recalled that leaf shape differences of the two subspecies are found not only in the relative width of the blade at the upper and lower quarter lengths but also in the fact that the blade predominantly is cuneate in *A. t. tuberosa* (fig. 3, center figure) and cordate in *A. t. interior* (fig. 3, right figure). To measure either character it is found desirable to draw a horizontal line at right angles to the median line *OB* at one quarter the distance of its length from the apex *(XX')* and base *(YY')*, respectively.

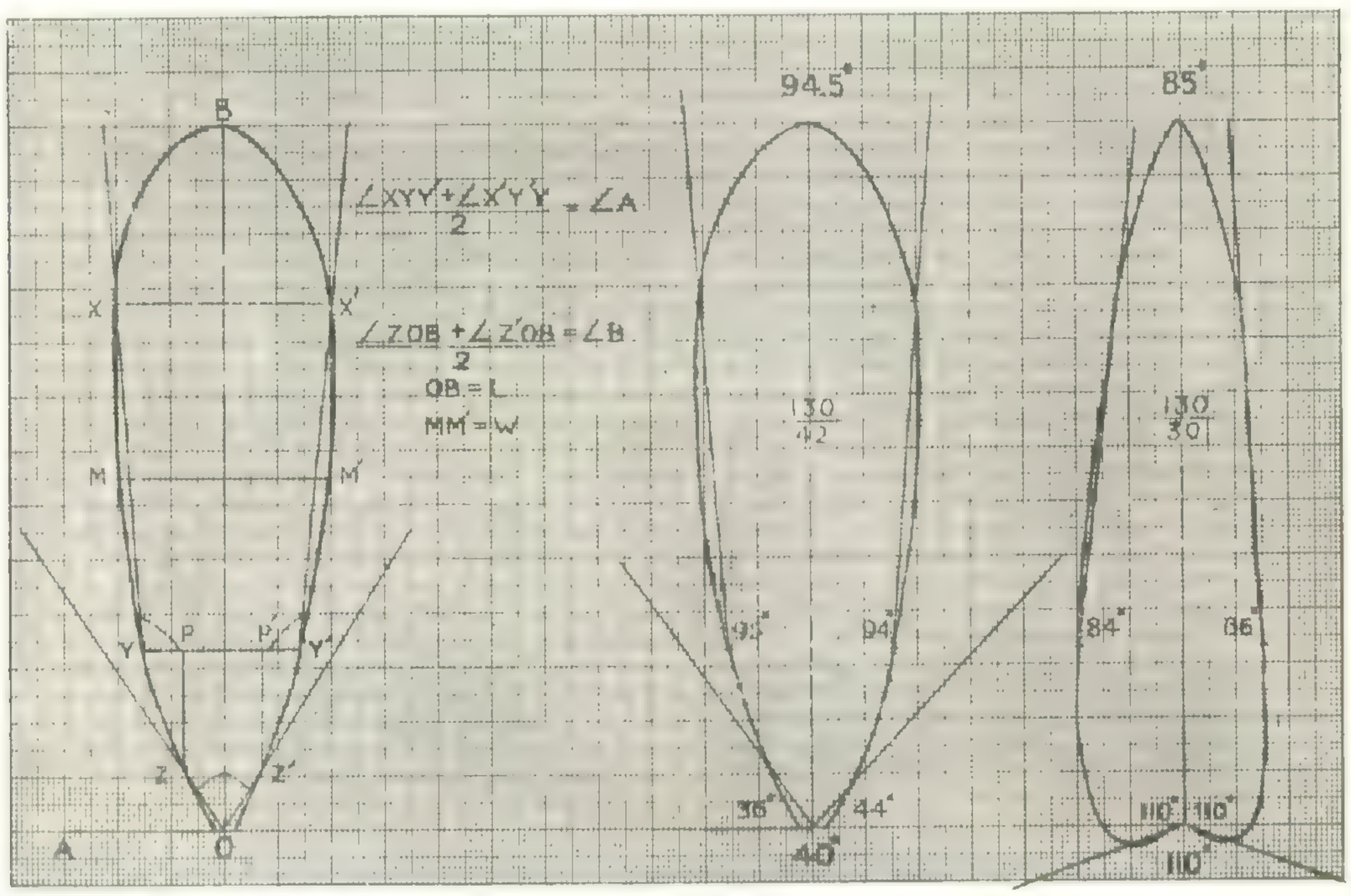


Fig. 3. Methods for measuring leaf shape in butterflyweeds.—Explanation in the text.

In order to measure the direction and extent of apical taper of the leaves two chords now are drawn, *XY* and *X'Y'*. Using a standard protractor the two angles *XYY'* and*X'Y'Y* are measured to the nearest degree, rounding to the nearest even figure, and their mean is entered as the statistic hereafter to be known as ∠A.

In fig. 3 it will be seen that measurements of ∠A are 94.5° and 85° (treated as 85.0° in computations) for *A. t. tuberosa* and *A. t. interior* respectively. By use of this type of measure, a plant taxonomist will recognize that a leaf of ovate type will always have an angular reading of less than 90°, a leaf of obovate type one of more than 90°, and a leaf exactly of oblong type a reading of exactly 90°.

An angular measure to distinguish different types of leaf base in butterflyweed was obtained after it was recognized that in cordate leaves the tip of the basal lobe usually occurs at a point about midway between *O* and *Y* on the one side, and between *O* and *Y'* on the other. Consequently, I now drop two perpendiculars *PZ* and *P'Z'* at points on *YY'* midway between *OB* and the margin of the leaf as indicated in the diagrams to the left of fig. 3. The angles *ZOB* and *Z'OB* are now

read by protractor as before, and the mean rendered as ∠B, the measure of the leaf base. In the diagrams to the center and right of fig. 3 it is seen that the example for the cuneate base of ssp. *tuberosa* has an ∠B value of 40° while the equivalent value for the cordate base of ssp. *interior* is 110°. A truncate base would have an ∠B of 90°. In computations these figures are recorded as though significant to one decimal.

It will occur to the reader that the values ∠A and ∠B actually refer to hypothetical leaf halves and thus are not real variables. Such is doubtless the case, but their other virtues will probably save them from being condemned by the practical statistician. In addition, my recording of the mean angles to one decimal in excess of significant digits is open to criticism although I believe it will be allowed since subsequent computations are limited to one decimal. In practice the process of averaging, besides halving the scale intervals, has the effect of halving the experimental error.

Although ∠A and ∠B have been very satisfactory as measures for shape in *A. t. tuberosa* and *A. t. interior*, I must confess that they are wholly inoperative with respect to *A. t. Rolfsii*. This has been a great disappointment, although to be anticipated since one could scarcely expect to differentiate three value ranges and all their intermediates upon a linear scale. This is an unfortunate consequence of the biological reality of *Rolfsii*. It might be possible to exclude *Rolfsii* from the absolute comparison of *tuberosa* and *interior* and yet to contrast it with both by means of an additional system of arbitrary scores, say for the crisped margin of the leaf. This would mix a discrete with four continuous scales, however, and the result probably would not be very helpful.

There can be little doubt that *Rolfsii* interbreeds with both *tuberosa* and *interior* upon the southeastern coastal plain, and it would be interesting to be able to measure the phenomenon accurately. It is possible to do so only indirectly according to my methods. In further studies we shall not forget the role that *Rolfsii* undoubtedly plays, particularly with regard to introgression with the other two subspecies, but we will be able to deal with it only through inference.

ESTIMATES OF EXPERIMENTAL ERROR

The methods just described at one time appeared so crude to me, compared to the technical refinements of others, that I spent some effort in obtaining estimates of the experimental error involved. Despite the risk of being tedious, I am reporting the results in some detail because I believe that exercises of this sort should be published more frequently. As a matter of fact, I know of only one other published estimate of experimental error of measurements used in population studies, that of Sumner (1927), in which the author was chiefly interested in variation of measurement amongst different observers.

In the summer of 1945 ten leaves of *Asclepias tuberosa interior* were collected along a roadside near Valley Park, St. Louis County, Missouri. They were placed in numbered envelopes and subsequently measured with respect to length, width,

∠A and ∠B, while in the fresh condition. After measurement, each leaf was returned to its proper envelope and dried under pressure for a week. For ten consecutive days thereafter the leaves were drawn and measured, being returned to their proper envelopes each time, but the order of the envelopes changed by shuffling. After the tenth dry measurement the leaves were boiled separately and measured a last time. In this experiment extra precaution was taken against unconscious bias in that I personally traced the outlines on each occasion, while my friend Richard W. Holm performed the actual measurements independently.

Table I contrasts the measurements of the ten leaves in the fresh condition and after having been boiled after drying. Table II presents the results of measuring the ten leaves upon ten different occasions. The first is designed to show, as far as this case is concerned, how comparable statistics obtained from fresh leaves and those from soaked herbarium specimens may be. The second is a gage of accuracy in the tracing and measuring process itself, and also provides something of a guide to the statistics of Table I.

TABLE I

MEASUREMENTS OF *ASCLEPIAS TUBEROSA INTERIOR* LEAVES WHEN FRESH AND AFTER SOAKING IN BOILING WATER

(Means, standard deviations, and coefficients of variation; angles in degrees, length and width in millimeters)

		∠A			∠B			Length			Width		
	N	$\bar{X}$	s	V	$\bar{X}$	s	V	$\bar{X}$	s	V	$\bar{X}$	s	V
Fresh	10	85.0	0.5	0.6	120.0	1.6	1.3	77.3	1.4	1.8	19.7	0.5	2.5
Soaked	10	85.2	0.4	0.5	120.6	2.1	1.7	76.1	1.3	1.7	19.3	0.5	2.6

Since I have no similar exercises with which to compare, it is hard to evaluate the results recorded in Table II. I was surprised indeed, however, when the error appeared to be so small, in view of my rather crude instruments, ranging from 0.4° or 0.4 per cent for ∠A to only 1.5° or 1.3 per cent for ∠B. The metric error likewise appears to be small. In comparing Table I with the discussion of Table II it is seen to be immaterial, as far as the two angles are concerned, whether the leaves are measured fresh, dry, or soaked, since all three means for both lie within the experimental error estimated in Table II. In length and width, on the other hand, the three means lie at distances greater than that provided for by the estimate of error, particularly in width. This is disquieting, but there is no recourse since it would be impossible to measure all leaves while fresh. Statistics of length and width, however, will play a role subordinate to those for the two angles in the studies which follow, since they are not important systematically.

TABLE II

MEASUREMENTS OF TEN DRIED LEAVES OF *ASCLEPIAS TUBEROSA INTERIOR* MEASURED ON TEN CONSECUTIVE DAYS

(Means, standard deviations, coefficients of variation, means of means, means of standard deviations, and means of coefficients of variation; angles in degrees, length and width in millimeters)

Leaf No.	∠A			∠B			Length			Width		
	$\bar{X}$	s	V	$\bar{X}$	s	V	$\bar{X}$	s	V	$\bar{X}$	s	V
1	85.2	0.2	0.2	118.9	1.2	1.0	76.0	0.0	0.0	20.0	0.0	0.0
2	85.2	0.4	0.5	117.2	2.0	1.7	75.2	0.4	0.5	18.0	0.0	0.0
3	85.1	0.3	0.4	119.1	1.9	1.6	75.9	0.4	0.5	18.6	0.5	2.7
4	85.3	0.3	0.4	121.5	1.4	1.2	75.4	0.5	0.7	19.0	0.0	0.0
5	85.4	0.4	0.5	119.6	2.7	2.2	75.6	0.5	0.7	18.7	0.5	2.7
6	85.2	0.6	0.7	114.0	1.2	1.0	73.2	0.4	0.5	19.0	0.0	0.0
7	85.3	0.4	0.5	117.2	1.1	0.9	74.0	0.0	0.0	18.1	0.3	1.7
8	85.1	0.2	0.2	120.6	1.3	1.1	77.1	0.3	0.4	19.1	0.3	1.6
9	85.1	0.5	0.6	113.9	1.6	1.4	75.3	0.5	0.7	18.1	0.3	1.7
10	85.1	0.3	0.4	121.8	1.0	0.8	72.6	0.8	1.1	18.0	0.0	0.0
$\bar{X}$	*85.2*	*0.4*	*0.4*	*118.4*	*1.5*	*1.3*	*75.0*	*0.4*	*0.5*	*18.7*	*0.2*	*1.0*

IV. The Phenocontours

Technique of mapping

Phenocontour mapping is such a recent biological technique that it may be worth while to combine the account of my own practice with some general comments. The subject may be divided into several considerations which impinge upon one another so closely that they form a sort of continuum. In beginning an investigation of this kind, the first thing to be done is to become familiar with the systematic morphology of the organism chosen for study. Without a clear understanding of the critical characters of the species, for example, much time may be spent measuring size which might be spent more profitably measuring shape. In plant subjects, recourse should be had to a large, well-ordered, general herbarium where the problem in all likelihood can be viewed in perspective and plans made for the most promising direction of attack.

Having selected a problem and noting the most advantageous direction of attack, suitable biometric measures must be devised as the *sine qua non* of all that is to follow. A measure must be found which expresses numerically the phenomena judged as biologically most significant. Any given measure will only infrequently be found effective for more than the organism for which it was invented. My method of measuring leaf base in *Asclepias tuberosa*, for example, may be quite useless in measuring that of another species.

A good measure should be duplicable, sensitive to organic variation, and should provide an unwarped scale. These are rather complex attributes to discuss briefly.

They discriminate, in my opinion, against various types of discontinuous scales encountered in arbitrary scoring. In some cases, as in presence-or-absence criteria, scoring is the only sensible procedure. In others, the varying characters may be so complex that scores at first would appear as the only recourse. But scores almost inevitably are the product of the personal equation and should be used only when standard scales, such as the linear and the angular, are unavailing. The statistical advantages of fixed continuous scales are expressed most succinctly by Miss Walker (1943): "In order to know how much of a trait an individual has or to say that one thing is twice another, it is necessary not only to have equality of units but also to establish a zero point. Only when these two conditions are met can scores properly be spoken of as measures."

The area chosen for mapping preferably should include the entire range of the species or other taxonomic unit under investigation. This sometimes will be very large and impose considerable handicap in the gathering of data. But as a general rule the biological interest will be proportional to the area because of the relative number of factors allowed to operate. When I commenced this study of butterflyweed several years ago, I seriously considered following a suggestion of Huxley and confining my efforts to a single profile across the distribution of the species. Luckily my taxonomic training insisted that the distribution be treated as a whole; several unsuspected topics of interest emerged as a result.

Equal to the importance of adequate measures is that of adequate sampling. The prime requisite of sampling is that it be random. In biometric work of this kind, one cannot use the word "random" in quite the same sense in which it is employed in ordinary statistics; one cannot make use, for example, of the published lists of random numbers commonly employed in sampling. It is necessary to avoid the selection of cases which exhibit injury or manifest growth abnormality. It is necessary also to select cases at equivalent stages of development; therefore I have selected leaves from about the middle of a flowering stem rather than leaves at a given node from the top or bottom of the stem, for some stems produce a larger number of nodes during the course of their development than do others. Above all, one must not allow himself to select what he chooses to call "typical" cases in the hope of deriving therefrom the benefits of random sampling.

It does not seem quite possible to deal with questions of bias here in the ordinary way. In my own studies I think of bias as being intellectual, accidental, or biological. The intellectual bias is understood easily as the more or less subconscious desire to vindicate a predisposition. Perhaps its best antidote is to remember that truth may be stranger than fiction. Accidental bias may be occasioned by the paucity of specimens available for study in a given population. If herbarium specimens are in use it may be occasioned by duplicated specimens frequently encountered. Protection is taken against this by keeping a list of collectors' numbers as in ordinary monographic work. A variety of other sources of accidental bias come to mind.

Biological bias is a phenomenon which is less easy for a mathematical statistician to anticipate. In plants, if a species forms true clons it may be difficult if not impossible to tell whether one actually is sampling a number of genetic individuals or offshoots from a single plant. Fluctuations of climate are known to have a pronounced effect upon phenotypic expression (Lewis, 1947), and a sampling made during any given season or year may be biased as a result. Sampling made for convenience along roadsides or in occupied areas may present a very special bias (Wiegand, 1935). On first consideration it might be thought possible to escape physiological bias if sampling of an organism were made at random stages of its seasonal growth. But if any sample is allowed to consist chiefly of cases collected during a given stage of development, it may be biased with respect to others made during another stage. I have limited my sampling of butterflyweed to plants in full anthesis.

The number of samples and number of cases included is secondary in importance to the degree of randomness obtained. However, it may be worth while to emphasize that an adequate sampling is dependent more upon the number and randomness of samples than upon the number of included cases. Of course I do not overlook the fact that reliability of means and their derived statistical measures of variability increases as a rule with sample size; but size alone is not an indication of randomness and hence of reliability. Adequacy of sample size is determined by the unique degree of variability of each organism and can be determined in each case only after special observation.

Adequate sampling of the vast distribution of such a species as *Asclepias tuberosa*, an area of approximately 1,500,000 square miles, is clearly beyond the power of a single individual since we require randomness of climate, time, and environment. In an earlier section of this paper I have explained how herbarium collections would appear to satisfy these conditions. The argument may be advanced, however, that the relatively small numbers of specimens available in herbaria is insufficient for an adequate sampling distribution. Superficially it appears small indeed. Its adequacy with regard to butterflyweed may be judged by fig. 7 of this paper, in which statistics of two sets of samples are compared: one from the herbarium, consisting of 117 cases distributed along an approximately 1200-mile profile from Topeka, Kansas, to Norfolk, Virginia, and the other of 994 cases collected personally by myself and two friends in June, 1946, along roadsides between those two cities. The close correspondence and consistency of the two samplings are striking.

If I may extend my comments on sampling a bit further, I should like to call attention again to the area inhabited by *A. tuberosa*: approximately 1,500,000 square miles. First impulse might be to obtain statistics from whatever source and to combine them for the supposed benefits of larger samples. I am obliged to confess that for this vast area I have been able to collect and measure only approximately 12,000 cases in the time at my disposal, or about 1 per 115 square

miles. At first glance this appears inadequate indeed, and it minimizes the true situation since the cases could not, for practical reasons, be distributed uniformly. Actually my samples fall into three rough categories: cases obtained from herbarium specimens, those collected along roadsides, and those obtained in hit-or-miss fashion throughout the whole species distribution, largely through the kindness of interested friends.

Cases obtained from these three sources surely cannot be combined, since they have been accumulated under different conditions, and their discrepant numbers would constitute a serious bias. Consequently I have kept them separate although using all for comparison according to the special values accrued from each. At the risk of over-emphasis, I should like to repeat that of these three categories of samples, I consider that obtained from herbarium material by far the most representative biologically although they are also the smallest numerically, numbering only about 3,000 cases, or somewhat less than 1 per 470 square miles of the specific distribution. As shocking as this ratio will appear, I believe the derived statistics, on the whole, to be biologically reliable, and I have used them in constructing my phenocontour maps to the exclusion of other data.

The projection of data upon a phenocontour map is a rather complex matter which depends upon such factors as amount of available statistics, size and character of the area involved, and nature of the information which it is desired to convey. In his study of pelage melanism in the Tasmanian bush opposum, *Trichosurus vulpecula fuliginosus*, Pearson (1938) employed relative percentages of two class scores, black and gray, although he mentions unmeasured variation in both. By using commercial pelt records of approximately 105,000 cases distributed amongst 48 more or less equally spaced stations, a ratio of about 5 cases per square mile, he was able to plot a series of four contours ("isophenes" of Huxley) approximately separating areas including 0–25 per cent, 25–50 per cent, 50–75 per cent, and 75–100 per cent of gray pelts. His conclusions are chiefly historical.

Few biologists will be able to equal the volume of Pearson's data. To be as representative of distribution for *Asclepias tuberosa*, my records would have to embrace over 7,000,000 cases, instead of the approximately 3,000 which I have! Another advantage of Pearson's data is the distribution of cases amongst 48 rather equally spaced stations.

Readers familiar with the composition of a general herbarium already are aware that the geographical distribution of exsiccatae, even in the United States, is far from uniform. Greatest concentrations of specimens occur as a rule about well-established cities where botanists long since have resided. Next come states which have undergone systematic botanical surveys, and there is a gratifying number of these. Thirdly, there are regions of peculiar scenic or biological interests, such as our national parks, which attract appreciable numbers of plant collectors. But we cannot disregard areas, sometimes of considerable extent, where a lamentable hiatus

of herbarium records is encountered. There is no fixed pattern to this mosaic, and it presents the major obstacle in phenocontour mapping from herbarium collections.

The projection of data upon a phenocontour map presumably should require the imposition of equidistant statistics from equal areas. I have accomplished this by dividing the species distribution into quadrats of equal areas for which I have combined the data secured from the various localities included within each. This, of course, creates a system of artificial (in contrast to natural) populations from which the desired statistics are computed.

The quadrat area chosen clearly depends upon the geographic plasticity of the species and the nature of the information desired. If the species is very responsive to altitude or ecology, the size of the quadrat will need to be much smaller than if the organism is not so sensitive. This may be a very serious obstacle in mapping a large area. Fortunately, *Asclepias tuberosa* appears to be rather indifferent in these respects, and the size of the quadrat depends chiefly upon the necessity of obtaining artificial populations equally distributed and yet of sufficient numbers for statistical analysis. This amounts to a certain guise of "gerrymandering," but is legitimate since the same quadrat area is employed throughout.

In this study of butterflyweed I have manipulated quadrat area to the end of obtaining populations of at least five cases in critical but poorly collected regions. The quadrats in this instance are approximately 120 miles square, and there are 136 within the range of *A. t. tuberosa* and *A. t. interior*—many fewer than I would wish. Even with these large areas, it will be seen that certain of them have failed to yield as many as five cases. After recording the quadrat data, isophenes may be drawn, if desired or possible, either connecting equal statistics or according to arbitrary ranges, as practiced by Pearson.

The nature of statistics projected upon the map will vary with individual problems and with the inclination of investigators. If scores are used, Pearson's system, already explained, would appear admirable. If a continuous scale has been employed in measurement, it will be natural to compute the mean; and from it may be derived any of the familiar measures of dispersion such as the standard deviation and the coefficient of variation. These may be entered on the map together with the mean. A measure of variability frequently will be necessary in order to interpret the geographical distribution of means.

Of course there is a vast number of statistical formulae which may be used for the analysis of biological measurement, and if one has a taste for mathematics the possibilities are endless. In my own study, after some dalliance, I have limited myself, as a rule, to the simple calculation of means, standard errors, standard deviations, and coefficients of variation, the second and fourth largely for the sake of convention. An outstanding example of another point of view is afforded by

Czeczottowa's (1933) remarkably painstaking study of variation in beech leaves, to which Dr. M. K. Elias kindly has called my attention.

In the phenocontour maps which follow, quadrats containing five or more cases are indicated with the mean in large bold face type and the associated standard deviation in large italics. Means of quadrats containing less than five cases are printed in small Roman type. The standard deviation is used instead of the coefficient of variation because there appears to be no need for percentage comparison; also the former adapts itself more readily to my procedure, and the latter appears too sensitive to the relative magnitudes of the means, in addition to other disadvantages (cf. Kesteven, 1946).

INTERPRETATION OF THE MAPS

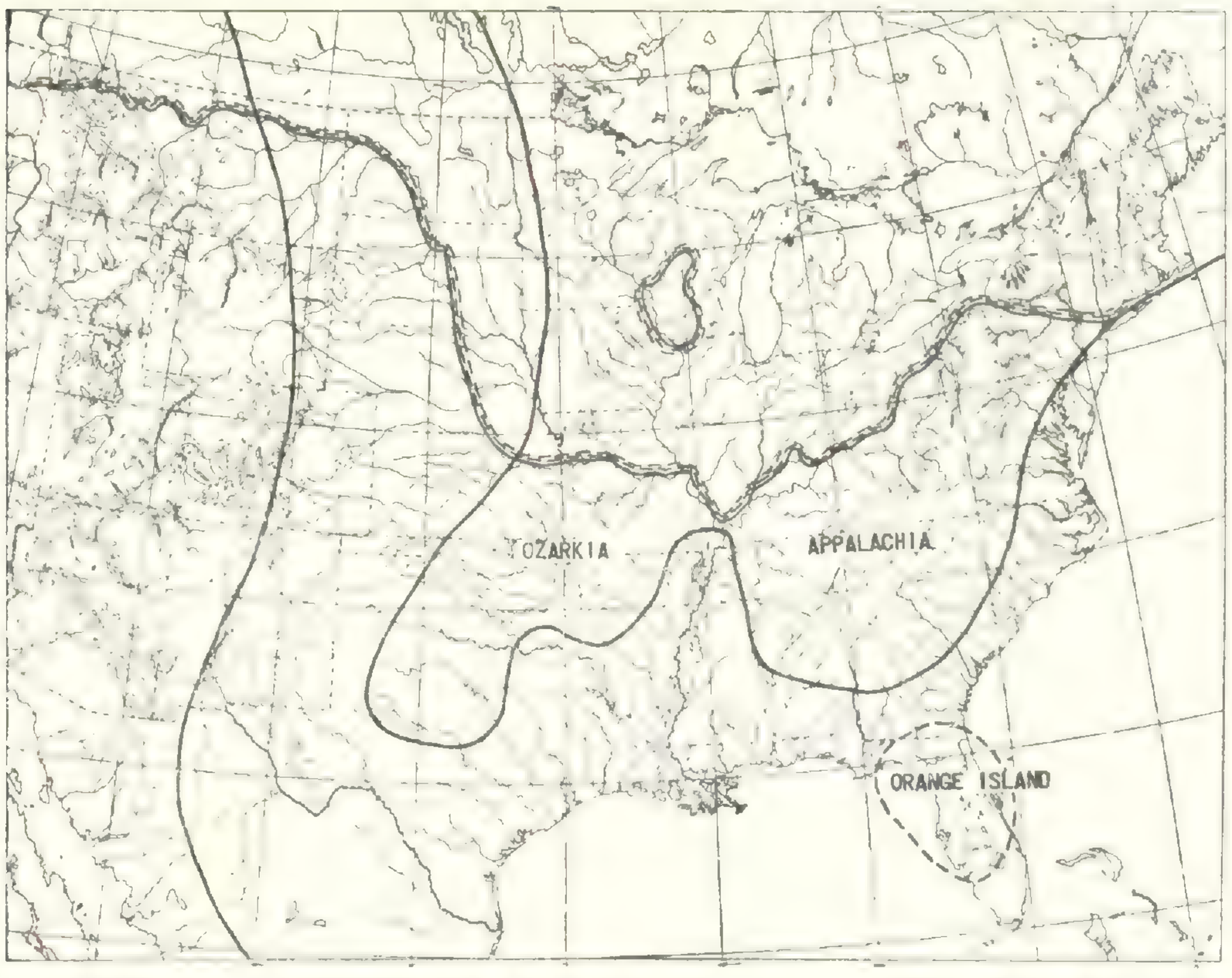
INTRODUCTION

Before turning to the phenocontour maps, it may be well to consider very hastily certain details of the paleogeography of eastern North America which will have a bearing on our interpretations of the population dynamics of *Asclepias tuberosa*. The discussion is illustrated by Map II.

It is generally recognized that many of the principal families of Flowering Plants were established by the close of the Mesozoic era, possibly before the Lower Cretaceous. Although I know of no indubitable fossil remains of *Asclepias*, numerous records of Late Cretaceous and Mesozoic imprints, such as the form genus *Apocynophyllum*, are known which may well represent, at least in part, ancestors of our modern milkweeds, if not records of extant species. At any rate, present distributions of many species of *Asclepias* correspond so closely to what is known of Cretaceous geography that I feel we may hypothesize rather safely much the same speciation in those times as that with which we are familiar at present (cf. Woodson, 1947).

The Cretaceous has been called "the age of greatest submergence of the continents and the most extensive epeiric seas the Earth has known (Schuchert & Dunbar, 1933)." The complex submergences and resulting isolation of floras probably were of the utmost importance to the meteoric evolutionary diversification of Angiosperms during this time, and are reflected in present speciation.

Late Cretaceous saw the climax of the dissection of North America with the submergence of the Rocky Mountain trough from the Caribbean to the Arctic. This was accompanied by submergence of the southeastern coastal plain, particularly north of the Gulf of Mexico, a deep embayment extending up the present Mississippi valley as far as southern Illinois. This embayment separated the ancient Appalachian and Ozark plateaus, including the extension of the latter to the Llano uplift in central Texas, and is recalled in our present vegetation by numerous vicarious species and subspecies. Amongst these may be mentioned *Asclepias t. tuberosa* and *A. t. interior*, respectively.

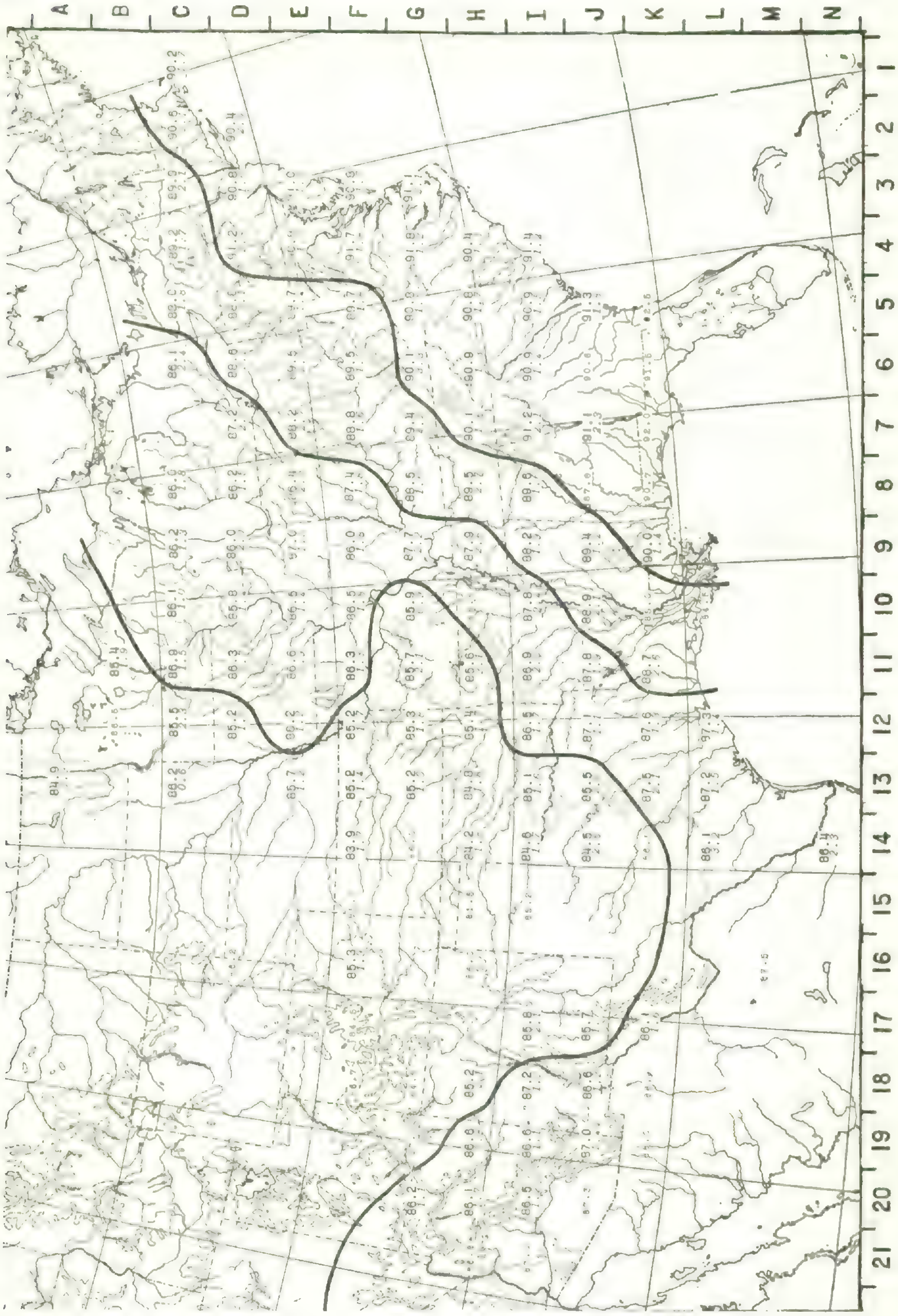


Map II. Ozarkia, Appalachia, and Orange Island, with reference to the Cretaceous and early Mesozoic seas, and Pleistocene glaciation. Explanation in the text.

Of equal interest in this connection is the probably fluctuating emergence of low islands in what is now northern Florida, culminating in the early Cenozoic in the appearance of the more sizable "Orange Island," separated from the Georgian coast by the Suwanee strait (Schuchert, 1935). On these islands possibly developed many or most of the Floridian endemics of Appalachian affinity, including *A. t. Rolfsii* and numerous other milkweeds.

Withdrawal of the Cretaceous seas during the early Cenozoic effected the reunion of the Appalachian and Ozarkian lands in Oligocene, and of emergent Orange Island to the continent in Pliocene. By Pliocene, therefore, there apparently were no geographic barriers to reunion of the disjunct distributions of the three subspecies of *Asclepias tuberosa,* if indeed they existed at that time.

Pleistocene brought the continental ice sheets approximately to the present valleys of the Missouri and Ohio rivers, virtually to the head of the old Mississippi embayment of Cretaceous and early Cenozoic times. This undoubtedly provided a partial secondary separation of the putative ranges of *A. t. tuberosa* and *A. t. interior.* It is well known that four glacial periods occurred during Pleistocene, interspersed by warm interglacials longer, indeed, than the present day is removed from the last withdrawal of the ice. The time since the retreat of the Wisconsin ice sheet usually is reckoned at about 25,000 years.



Map III. *Asclepias tuberosa*: phenocontour system of ∠A (apical taper of leaves). Explanation in the text.

These well-known facts are outlined to give perspective for what we are to find in the population dynamics of *Asclepias tuberosa* in recent times. They underline the possibility that the phenomena which we will discuss are not unique to the present, but perhaps the repetition of past and similar phenomena. It is difficult indeed to estimate the effect of such repetitions upon population genetics, but at least they should not be disregarded.

∠A

The phenocontours for ∠A which are reproduced in Map III are projected according to quadrats 120 miles square, as has been explained previously, with the means of quadrat populations including five or more cases printed in large bold-face numerals and the associated standard deviations immediately below in large italics. Means of quadrat populations including less than five cases appear in small Roman-type numerals. Three isophenes have been drawn approximately separating bold-face means included within intervals of 2° from the Atlantic coast. Statistical sources for the data used in compiling this map, as well as for the three which follow, are presented in Table III.

It may be considered that the 90°–91° contour represents the range of "true" *A. t. tuberosa,* while that of "true" *A. t. interior* is indicated by the 84°–85° contour. The 88°–89° and the 86°–87° contours represent subspecific intermediates except the populations in the far southwest and for the most part in the northern Mississippi valley which, for reasons to be developed later, are regarded as affected by intra-subspecific differentiation. Data for *A. t. Rolfsii* regrettably are absent for reasons already explained.

After the preceding discussion of paleogeography, it is easy to identify the central portions of the "true" subspecies distributions as centering in general on the Appalachian and Ozarkian-Llanoan headlands of Late Cretaceous time. Between these centers a broad cline stretches from the Great Lakes to the Gulf of Mexico, broader in the northern and abruptly constricted in the southern halves.

The most obvious explanation of this cline is the hybridization of individuals of either subspecies at the commissure of their distributions with continuous backcrossing to obtain the remarkably broad phenotypic gradient presented by the map. This process has been termed "introgressive hybridization" by Anderson and Hubricht (1938), shortened to "introgression" by some recent writers, and the result is a genocline (Huxley, 1942).

The middle isophene apparently represents the mid-current of gene flow between the two subspecies. Its virtually straight course is striking, and possibly would suggest nearly equal introgressive pressure from east and west. The nearly rectilinear nature of this isophene is the only evidence that will be presented at this time to support my assertion that the peculiar course of the western isophene is due to intra-subspecific forces operating within *A. t. interior*, and not to intro-

TABLE III

LEAVES OF *ASCLEPIAS TUBEROSA* (SENSU LAT.) FROM HERBARIUM MATERIAL ASSEMBLED INTO EQUAL-AREA QUADRATS ACCORDING TO GEOGRAPHIC PROVENIENCE

(Means, standard errors, standard deviations, and coefficients of variation; angles in degrees, length and width in millimeters)

Quadrat	N	∠A			∠B			Length			Width		
		$\bar{X}$	s	V	$\bar{X}$	s	V	$\bar{X}$	s	V	$\bar{X}$	s	V
A-13	5	84.9 ± 0.4	0.9	1.1	95.2 ± 7.3	14.7	15.4	79.8 ± 3.6	7.3	9.1	13.0 ± 1.8	3.7	28.5
B-3	4	90.0			40.9			83.5			12.8		
B-11	9	85.4 ± 0.7	1.9	2.2	84.7 ± 4.8	13.4	15.8	79.4 ± 2.4	6.9	8.7	13.0 ± 1.4	3.9	30.0
B-12	3	86.5			100.0			78.0			8.7		
C-1	21	90.2 ± 0.4	1.7	1.9	48.4 ± 3.0	13.2	27.3	68.8 ± 2.9	12.9	18.8	14.6 ± 1.1	5.0	34.2
C-2	60	90.6 ± 0.3	2.1	2.3	48.1 ± 2.0	15.0	31.2	79.3 ± 2.1	16.4	20.7	17.8 ± 0.8	5.8	32.6
C-3	23	89.9 ± 0.4	2.1	2.3	63.3 ± 4.0	18.6	29.4	89.2 ± 3.7	17.4	19.5	17.8 ± 0.9	4.3	24.2
C-4	26	89.2 ± 0.3	1.7	1.9	64.0 ± 4.5	22.6	35.3	82.2 ± 2.7	13.6	16.5	12.9 ± 0.8	3.8	29.4
C-5	14	88.0 ± 0.5	1.8	2.0	74.7 ± 5.4	19.4	26.0	85.4 ± 4.8	17.1	20.0	15.4 ± 1.3	4.8	31.2
C-6	9	86.1 ± 0.8	2.4	2.8	83.6 ± 4.7	13.3	15.9	73.7 ± 5.2	14.6	19.8	15.3 ± 1.2	3.4	22.2
C-8	20	86.0 ± 0.4	1.8	2.1	84.4 ± 4.2	18.2	21.6	74.2 ± 1.9	8.4	11.3	12.8 ± 0.8	3.6	28.1
C-9	12	86.2 ± 0.4	1.3	1.5	84.9 ± 6.4	21.3	25.1	78.7 ± 3.5	11.5	14.6	11.8 ± 1.4	4.8	40.7
C-10	16	86.1 ± 0.3	1.0	1.2	91.3 ± 4.3	16.6	18.2	77.8 ± 3.1	12.1	15.6	12.5 ± 1.1	4.1	32.8
C-11	40	86.9 ± 0.2	1.5	1.7	97.3 ± 3.0	18.9	19.4	83.2 ± 2.1	13.1	15.7	11.0 ± 0.5	3.2	18.7
C-12	11	85.5 ± 0.7	2.3	2.7	92.6 ± 4.2	13.4	14.5	81.1 ± 4.6	14.4	17.8	12.0 ± 1.3	4.2	35.0
C-13	5	86.2 ± 0.3	0.6	0.7	95.8 ± 8.1	16.3	17.0	74.8 ± 6.6	13.2	17.6	11.6 ± 0.9	1.8	15.5
D-2	38	90.4 ± 0.3	2.0	2.2	56.9 ± 3.6	21.9	38.5	77.4 ± 1.9	11.4	14.7	17.0 ± 0.8	5.1	30.0
D-3	61	90.8 ± 0.2	1.6	1.8	56.6 ± 2.3	17.6	31.1	73.9 ± 2.1	16.2	21.9	16.9 ± 0.7	5.2	30.8
D-4	30	91.2 ± 0.5	2.8	3.1	58.0 ± 4.8	25.8	44.5	83.4 ± 2.9	15.7	18.8	16.6 ± 1.0	5.2	31.3
D-5	6	88.8 ± 1.4	3.1	3.5	66.0 ± 14.4	32.3	48.9	107.3 ± 11.1	24.8	23.1	19.3 ± 3.2	7.2	37.3
D-6	10	88.6 ± 0.7	2.2	2.5	77.2 ± 8.3	25.0	32.4	86.2 ± 4.7	14.2	16.5	16.1 ± 1.6	4.7	29.2
D-7	39	87.2 ± 0.3	2.0	2.3	82.6 ± 3.4	21.1	25.6	83.6 ± 2.6	16.2	19.4	15.0 ± 0.7	4.6	30.7
D-8	36	86.2 ± 0.2	1.5	1.7	96.4 ± 4.9	29.1	30.2	81.0 ± 2.1	12.4	15.3	15.4 ± 0.7	4.0	26.0
D-9	31	86.0 ± 0.4	2.0	2.3	95.0 ± 2.6	14.2	14.9	80.8 ± 2.1	11.7	14.5	12.2 ± 0.6	3.1	25.4
D-10	19	85.8 ± 0.3	1.4	1.6	93.3 ± 3.4	14.6	15.6	84.7 ± 3.0	12.7	15.0	13.9 ± 0.8	3.5	25.2
D-11	26	86.3 ± 0.2	0.7	0.8	105.5 ± 2.1	10.5	10.0	80.1 ± 3.3	16.6	20.7	11.5 ± 0.7	3.5	30.4

TABLE III *(Continued)*

Quadrat	N	∠A			∠B			Length			Width		
		$\bar{X}$	s	V	$\bar{X}$	s	V	$\bar{X}$	s	V	$\bar{X}$	s	V
D-12	30	85.2 ± 0.2	1.0	1.2	108.5 ± 2.4	12.8	11.8	72.2 ± 1.5	8.1	11.2	11.8 ± 0.6	3.0	25.4
D-16	2	86.2			91.5			77.0			13.0		
E-3	106	91.0 ± 0.2	1.6	1.8	49.0 ± 1.6	16.9	34.5	68.3 ± 1.3	12.9	18.9	15.8 ± 0.4	4.7	29.6
E-4	67	90.8 ± 0.2	1.6	1.8	53.7 ± 2.1	16.8	31.3	73.2 ± 2.0	16.1	22.0	17.3 ± 0.6	5.0	28.9
E-5	76	89.7 ± 0.2	1.4	1.6	57.0 ± 1.9	17.0	29.8	82.3 ± 1.8	15.8	19.2	13.8 ± 0.5	4.7	34.1
E-6	18	89.5 ± 0.5	2.0	2.2	71.5 ± 4.9	20.1	28.1	95.3 ± 3.2	13.4	14.1	18.4 ± 1.2	5.1	27.7
E-7	13	88.2 ± 0.8	2.7	3.1	68.0 ± 4.4	15.1	22.2	83.7 ± 4.4	15.3	18.3	15.9 ± 1.7	5.8	36.5
E-8	48	86.4 ± 0.1	2.0	2.3	96.2 ± 1.1	17.3	18.0	83.5 ± 1.0	15.8	18.9	15.0 ± 0.6	4.2	28.0
E-9	50	87.0 ± 0.2	1.3	1.5	99.0 ± 2.0	14.1	14.1	75.0 ± 1.8	12.8	17.1	12.5 ± 0.5	3.6	28.8
E-10	23	86.5 ± 0.3	1.4	1.6	98.5 ± 3.0	13.9	14.1	85.5 ± 2.7	12.7	14.8	14.6 ± 0.7	3.2	21.9
E-11	11	86.6 ± 0.3	0.9	1.0	103.7 ± 2.9	9.3	8.0	70.5 ± 3.7	11.6	16.4	10.3 ± 1.0	3.3	32.0
E-12	10	86.2 ± 0.2	1.2	1.4	112.2 ± 4.2	12.7	11.3	70.5 ± 3.7	11.0	15.6	9.9 ± 0.8	2.5	25.2
E-13	37	85.7 ± 0.2	1.2	1.4	103.2 ± 1.7	10.0	9.7	74.3 ± 1.8	10.8	14.5	12.8 ± 0.5	3.2	25.0
F-3	8	90.8 ± 0.6	1.7	1.9	55.4 ± 4.0	10.6	19.1	70.2 ± 4.9	13.2	18.5	16.9 ± 1.8	4.7	28.6
F-4	15	91.7 ± 0.5	1.8	2.0	58.7 ± 4.2	15.8	27.9	70.0 ± 2.4	8.8	12.6	17.3 ± 0.9	3.5	20.1
F-5	34	89.7 ± 0.3	1.8	2.0	57.5 ± 3.2	18.0	31.3	78.6 ± 3.1	17.5	23.5	14.6 ± 0.8	4.5	30.8
F-6	32	89.5 ± 0.3	1.5	1.7	61.5 ± 3.1	17.8	20.9	84.7 ± 3.4	18.7	22.1	15.0 ± 0.8	4.2	28.0
F-7	24	88.8 ± 0.3	1.6	1.8	73.0 ± 4.5	21.6	29.6	80.0 ± 2.5	11.9	14.9	15.9 ± 0.8	3.6	22.6
F-8	20	87.4 ± 0.4	1.8	2.1	94.4 ± 4.3	18.7	19.8	90.7 ± 2.8	12.0	13.2	17.8 ± 1.0	4.5	25.2
F-9	26	86.0 ± 0.4	1.8	2.1	98.3 ± 2.9	14.5	14.8	84.4 ± 2.4	11.9	14.1	16.1 ± 1.0	4.8	29.8
F-10	30	86.5 ± 0.3	1.8	2.1	101.8 ± 2.6	13.8	13.6	76.1 ± 2.4	13.0	17.1	16.6 ± 0.9	4.7	28.3
F-11	26	86.3 ± 0.3	1.3	1.5	103.4 ± 1.7	8.3	8.0	79.5 ± 2.0	9.9	12.5	14.6 ± 0.7	3.5	24.0
F-12	29	85.2 ± 0.3	1.7	2.0	109.8 ± 1.8	9.4	8.6	72.9 ± 1.5	8.1	11.1	12.3 ± 0.5	2.7	22.0
F-13	27	85.2 ± 0.3	1.4	1.6	101.2 ± 2.1	10.5	10.4	67.5 ± 2.4	12.1	17.9	12.6 ± 0.7	3.5	27.8
F-14	20	83.9 ± 0.4	1.7	2.0	103.2 ± 1.8	8.2	7.9	58.1 ± 2.2	9.6	16.2	11.4 ± 0.8	3.5	30.7
F-15	1	85.0			96.5			71.0			14.0		
F-16	13	85.3 ± 0.5	1.9	2.2	80.3 ± 6.1	21.0	26.2	71.7 ± 3.9	13.5	18.8	13.0 ± 1.2	4.2	32.3
F-17	1	84.5			93.5			83.0			18.0		
F-18	3	86.7			83.5			76.7			9.0		
G-3	50	91.1 ± 0.3	2.1	2.3	52.8 ± 2.8	19.6	37.1	63.9 ± 1.8	12.4	19.4	14.4 ± 0.7	4.9	34.0
G-4	25	91.8 ± 0.2	1.2	1.3	55.3 ± 3.4	16.5	29.8	58.3 ± 2.3	11.1	19.0	12.0 ± 0.6	2.9	24.1

TABLE III *(Continued)*

Quadrat	N	∠A			∠B			Length			Width		
		$\bar{X}$	s	V	$\bar{X}$	s	V	$\bar{X}$	s	V	$\bar{X}$	s	V
G-5	18	90.8 ± 0.4	1.5	1.7	50.8 ± 3.3	13.8	27.2	80.1 ± 4.9	20.3	25.3	15.4 ± 1.1	4.5	29.2
G-6	6	90.1 ± 1.5	3.3	3.7	52.0 ± 5.5	12.3	23.7	69.3 ± 6.9	15.5	22.4	12.0 ± 1.5	3.4	28.3
G-7	11	89.4 ± 1.2	4.2	4.7	61.7 ± 6.7	21.1	34.2	80.9 ± 4.8	15.3	18.9	17.1 ± 1.8	5.6	32.7
G-8	11	88.5 ± 0.5	1.6	1.9	89.1 ± 6.1	19.3	21.7	90.6 ± 4.4	14.0	15.5	20.2 ± 1.5	4.8	23.8
G-9	22	87.7 ± 0.5	2.2	2.5	92.9 ± 3.7	16.8	18.1	82.5 ± 3.5	16.2	19.6	18.9 ± 1.2	5.8	30.7
G-10	12	85.9 ± 0.3	0.9	1.0	100.5 ± 1.7	5.5	5.5	84.4 ± 4.0	13.2	15.6	19.9 ± 1.2	3.9	19.6
G-11	12	85.7 ± 0.6	2.1	2.4	111.1 ± 2.0	6.6	5.0	76.1 ± 4.8	16.0	21.0	17.2 ± 1.5	5.0	29.1
G-12	19	85.3 ± 0.4	1.8	2.1	111.2 ± 1.5	6.3	5.7	64.2 ± 2.4	10.1	15.7	12.8 ± 1.0	3.1	24.2
G-13	8	85.2 ± 0.4	1.0	1.2	102.6 ± 4.5	12.0	11.7	67.4 ± 4.8	12.6	18.7	11.5 ± 1.3	3.7	32.2
G-14	1	86.0			102.0			58.0			10.0		
G-18	1	84.5			86.5			43.0			6.0		
G-19	2	87.0			68.8			63.0			7.5		
G-20	8	86.2 ± 0.4	1.1	1.3	83.6 ± 7.3	19.4	23.2	64.4 ± 5.9	15.6	24.2	8.4 ± 0.8	2.1	25.0
H-4	17	90.4 ± 0.3	1.3	1.4	57.4 ± 5.2	20.9	36.4	67.5 ± 2.8	11.2	16.6	13.6 ± 1.5	6.0	44.1
H-5	22	90.8 ± 0.4	1.7	1.9	54.1 ± 4.6	21.1	39.0	69.3 ± 3.0	13.7	19.8	12.8 ± 0.8	3.7	28.9
H-6	65	90.9 ± 0.2	1.3	1.4	52.6 ± 2.3	18.6	35.4	73.1 ± 1.7	13.4	18.3	15.3 ± 0.6	4.5	29.4
H-7	29	90.1 ± 0.3	1.6	1.8	49.6 ± 2.9	15.6	31.4	73.0 ± 2.3	12.3	16.8	16.5 ± 1.0	5.4	32.7
H-8	16	89.5 ± 0.7	2.7	3.0	58.2 ± 6.9	26.8	46.0	82.3 ± 4.6	17.8	21.6	16.1 ± 1.1	4.1	25.5
H-9	12	87.9 ± 0.8	2.6	3.0	77.3 ± 6.5	21.5	27.8	77.6 ± 4.4	14.5	18.2	18.6 ± 1.6	5.4	29.0
H-10	3	88.5			78.3			66.0			11.7		
H-11	17	85.6 ± 0.3	2.1	2.4	100.9 ± 1.9	13.1	12.0	69.4 ± 1.9	7.6	10.9	17.0 ± 1.2	4.6	27.1
H-12	26	85.4 ± 0.4	1.7	2.0	108.9 ± 2.0	9.8	9.0	70.2 ± 2.5	12.5	17.8	14.2 ± 0.9	4.4	31.0
H-13	38	84.8 ± 0.3	1.8	2.1	105.2 ± 1.6	9.8	9.3	64.5 ± 1.7	10.1	15.7	13.7 ± 0.7	4.3	31.4
H-14	16	84.2 ± 0.5	1.8	2.1	98.5 ± 2.9	11.4	11.6	63.4 ± 2.8	11.0	17.4	13.2 ± 0.8	3.2	24.2
H-15	2	81.5			112.0			69.0			16.0		
H-16	3	86.0			83.5			59.0			10.0		
H-17	3	87.0			86.0			57.7			6.7		
H-18	8	85.2 ± 0.8	2.1	2.5	88.1 ± 6.4	17.1	19.4	70.9 ± 2.7	7.1	10.0	11.9 ± 1.2	3.1	26.9
H-19	6	86.6 ± 0.4	0.8	0.9	87.5 ± 9.7	21.7	24.8	59.5 ± 5.8	13.1	18.6	7.0 ± 0.6	1.3	18.6
H-20	11	86.1 ± 0.5	1.7	2.0	83.8 ± 5.5	17.4	20.7	62.5 ± 3.6	11.3	18.1	8.3 ± 0.7	2.1	25.3
H-21	4	86.8			98.5			59.8			6.0		

TABLE III *(Continued)*

Quadrat	N	∠A			∠B			Length			Width		
		$\bar{X}$	s	V	$\bar{X}$	s	V	$\bar{X}$	s	V	$\bar{X}$	s	V
I-4	27	91.4 ± 0.2	1.2	1.3	47.7 ± 3.4	17.5	36.7	62.3 ± 2.8	14.4	23.1	12.1 ± 0.7	3.4	28.1
I-5	7	90.9 ± 0.6	1.5	1.6	47.6 ± 8.6	21.0	44.1	64.4 ± 9.0	22.0	34.1	9.7 ± 1.5	3.7	38.1
I-6	28	90.9 ± 0.3	1.4	1.5	50.6 ± 3.8	19.7	38.9	65.2 ± 2.3	11.8	18.1	14.5 ± 1.1	5.5	37.9
I-7	26	91.2 ± 0.4	2.1	2.3	49.5 ± 3.5	17.3	34.9	63.1 ± 1.8	8.9	14.1	14.9 ± 0.8	4.1	27.5
I-8	10	89.6 ± 0.5	1.6	1.8	63.0 ± 5.3	16.0	25.4	66.7 ± 2.6	7.8	11.7	16.1 ± 1.9	5.6	34.8
I-9	10	88.2 ± 0.6	1.9	2.2	83.9 ± 8.7	26.0	31.0	67.8 ± 6.9	20.7	30.5	14.2 ± 1.5	4.4	30.9
I-10	19	87.8 ± 0.6	2.4	2.7	92.4 ± 5.3	22.4	24.2	78.7 ± 3.9	16.7	21.2	14.2 ± 0.9	3.9	27.5
I-11	31	86.9 ± 0.4	2.0	2.3	99.5 ± 3.2	17.6	17.7	71.8 ± 2.8	15.3	21.3	13.6 ± 0.9	5.0	36.8
I-12	17	86.5 ± 0.4	1.7	2.0	99.4 ± 3.8	15.1	15.2	68.8 ± 3.3	13.2	19.2	11.5 ± 0.8	3.3	28.7
I-13	62	85.1 ± 0.2	1.6	1.9	108.4 ± 1.3	9.8	9.0	63.7 ± 1.2	9.6	15.1	13.1 ± 0.4	3.4	25.9
I-14	14	84.6 ± 0.5	1.7	2.0	105.9 ± 2.0	7.3	6.9	65.3 ± 2.9	10.5	16.1	13.5 ± 0.9	3.2	23.7
I-15	2	85.2			102.7			52.5			14.0		
I-17	8	85.8 ± 0.8	2.1	2.4	84.9 ± 6.1	16.0	18.9	58.9 ± 3.4	8.9	15.1	10.0 ± 1.2	3.1	31.0
I-18	8	87.2 ± 0.4	1.0	1.1	71.0 ± 4.1	10.8	15.2	67.5 ± 5.1	13.4	18.4	7.9 ± 0.8	2.2	27.8
I-19	8	86.5 ± 0.4	1.2	1.4	82.3 ± 5.3	13.9	16.8	63.5 ± 4.8	12.8	20.2	7.5 ± 1.0	2.7	36.0
I-20	7	86.6 ± 0.4	1.1	1.3	79.6 ± 5.2	12.7	16.0	65.6 ± 5.3	12.9	19.7	8.3 ± 0.5	1.2	14.4
I-21	4	87.0			80.7			65.0			8.2		
J-5	10	91.3 ± 0.6	1.8	2.0	49.6 ± 6.5	19.6	39.5	61.0 ± 6.5	10.9	17.9	11.6 ± 1.6	5.2	44.8
J-6	2	90.8			65.8			46.0			10.0		
J-7	21	91.1 ± 0.5	2.3	2.5	47.6 ± 5.3	23.9	50.2	58.2 ± 1.4	6.5	11.2	10.8 ± 0.6	2.7	25.0
J-8	2	87.8			82.8			81.0			18.0		
J-9	12	89.4 ± 0.4	1.2	1.3	80.8 ± 4.9	16.2	20.0	56.5 ± 3.0	10.1	17.9	11.1 ± 0.9	3.0	27.0
J-10	9	88.9 ± 0.7	2.1	2.4	86.4 ± 5.8	16.4	19.0	64.1 ± 2.4	6.9	10.8	15.2 ± 1.1	3.0	19.7
J-11	8	87.8 ± 0.7	1.9	2.2	73.6 ± 10.6	28.0	38.0	62.6 ± 4.5	10.7	17.1	10.6 ± 1.4	3.6	33.9
J-12	14	87.1 ± 0.3	1.1	1.3	86.4 ± 4.4	16.0	18.4	62.4 ± 4.0	14.3	22.9	12.4 ± 0.8	3.0	24.2
J-13	34	85.5 ± 0.3	2.0	2.3	94.1 ± 3.1	17.7	18.8	64.0 ± 1.6	9.0	14.1	12.7 ± 0.6	3.3	25.9
J-14	7	84.5 ± 1.1	2.6	3.1	84.1 ± 9.4	22.9	27.2	56.4 ± 6.3	15.4	27.3	12.0 ± 1.6	3.9	32.5
J-17	13	85.7 ± 0.5	1.7	2.0	83.9 ± 6.2	19.6	23.4	65.5 ± 5.0	15.9	24.3	10.5 ± 1.1	3.6	34.3
J-18	11	86.6 ± 0.4	1.2	1.4	87.7 ± 4.0	12.6	16.6	72.0 ± 5.7	18.1	25.1	8.8 ± 0.8	2.6	29.5
J-19	26	87.0 ± 0.3	1.4	1.6	79.4 ± 3.3	16.6	20.9	69.0 ± 3.7	18.6	26.9	8.2 ± 0.5	2.4	29.3
J-20	3	87.3			64.0			75.7			12.0		

TABLE III *(Continued)*

Quadrat	N	∠A			∠B			Length			Width		
		$\bar{X}$	s	V	$\bar{X}$	s	V	$\bar{X}$	s	V	$\bar{X}$	s	V
K-5	1	92.5			71.5			48.0			8.0		
K-6	1	91.5			53.0			60.0			10.0		
K-7	1	92.0			53.0			85.0			14.0		
K-8	3	90.7			65.3			65.0			12.3		
K-9	11	90.0 ± 0.4	1.4	1.6	69.1 ± 7.4	23.5	34.0	76.3 ± 5.8	18.4	24.1	13.2 ± 1.0	3.3	25.0
K-10	1	85.0			111.0			77.0			23.0		
K-11	11	88.7 ± 0.8	2.6	2.9	58.8 ± 6.2	19.5	33.2	58.1 ± 2.4	7.7	13.3	10.4 ± 0.9	2.8	26.9
K-12	18	87.6 ± 0.3	1.3	1.5	77.5 ± 4.3	17.6	22.7	58.6 ± 3.1	12.7	21.7	9.7 ± 0.6	2.6	26.9
K-13	13	87.5 ± 0.6	2.1	2.4	83.5 ± 5.7	19.6	23.5	54.5 ± 1.5	5.7	10.5	10.1 ± 0.5	1.8	17.8
K-14	1	86.5			106.0			75.0			18.0		
K-17	11	86.1 ± 0.5	1.6	1.8	79.4 ± 4.9	15.6	19.6	78.7 ± 0.4	14.2	18.0	12.3 ± 1.4	4.6	37.3
K-19	1	88.0			50.0			48.0			10.0		
K-20	4	86.9			86.1			59.7			6.0		
L-10	1	84.5			103.0			66.0			12.0		
L-12	11	87.3 ± 0.3	1.4	1.6	90.4 ± 3.8	11.9	13.2	54.6 ± 3.8	11.7	21.4	9.7 ± 1.2	3.7	38.2
L-13	27	87.2 ± 0.3	1.5	1.7	87.9 ± 4.6	23.4	26.6	54.3 ± 2.2	11.3	20.8	9.0 ± 0.6	2.9	31.1
L-14	7	86.1 ± 1.3	3.2	3.7	78.2 ± 6.1	14.8	18.9	50.0 ± 4.4	10.7	21.4	11.4 ± 1.6	4.0	35.1
M-16	1	87.5			46.0			51.0			6.0		
N-14	6	86.4 ± 1.0	2.3	2.6	68.8 ± 11.1	25.8	37.5	68.3 ± 6.5	14.5	21.2	7.0 ± 0.4	1.0	14.3

gression with the eastern subspecies. I consider the northeastern limit of "true" ssp. *interior* to approximate the converse of the northwestern limit of "true" ssp. *tuberosa*.

Attention has been called to the abrupt change of gradient of the genocline at approximately the middle. A paleogeographic explanation for this is seen in the fact that this location also approximates the southern terminus of the Pleistocene ice. North of this point, upon retreat of the ice, unusual opportunity for rapid migration must have been offered herbaceous plants with effective means of dissemination, such as milkweed with its comose seeds. Surely an unparalleled "open community" must have been offered them. Furthermore, the southern half of this cline traverses low, generally alluvial land unsuited to the species, where colonies are unusually sparse.

To this we must add obvious geographic features such as the more favorable climatic and edaphic conditions roughly north of this point. These factors apparently combine to explain why *Asclepias tuberosa* colonies of both subspecies are larger and more frequent roughly in the northern half of their ranges, as I have observed repeatedly. It is reasonable to expect more rapid gene flow, and consequently a more gradual cline, under such conditions than under those toward the south where the colonies are smaller and more widely separated.

Although the isophenes follow satisfactorily consistent courses, it is clear that both the individual quadrat means and their standard deviations would represent more or less distinctive population parameters within the broad intervals indicated. This also will be found true, but with different patterns, with regard to the other characters measured, as succeeding maps will show. Each quadrat population has its unique cell-like facets of mean tendencies and variabilities; all mutually dependent upon the constitution of their neighbor populations, but reflecting different internal forces. This heterogeneity within continuity will be found upon a lower level, but even more strikingly, in the account of natural populations which will follow.

The effects of introgression, therefore, are superimposed upon kaleidoscopic population patterns previously established by intra-subspecific gene flow in addition to diverse degrees of genetic drift; the latter, we may surmise roughly in inverse proportion to the former. I am inclined to discount any direct environmental effect on the expression of the two angular measures; but climatic and edaphic influence surely is exerted indirectly in moulding population tendencies in so far as it affects population size and frequency with regard to efficacy of gene flow, introgressive and otherwise.

The roles of population size and frequency in moulding population tendencies will be examined in more detail in another section of this paper. A preliminary intimation of their importance will be received upon examination in more detail of the quadrat statistics within the distribution of "true" *A. t. interior*, as indicated

by the map. In the Ozark region, where the subspecies is sufficiently frequent to be a roadside plant, the quadrat means for ∠A approximate a declination of 85.5°. The diminishing magnitude of the means as they progress toward the west suggests some slight, but diminishing, introgressive effect inadequately conveyed by the arbitrary isophene.

Near the boundary of the short-grass plains, population frequency drops abruptly, and the species ceases to be encountered commonly along roadsides. From this point some miles westward, one encounters a north-south distribution of plants with somewhat more sharply tapered leaves. As it happens, this tendency is associated with somewhat reduced length and somewhat increased width, so that a fairly recognizable race results.

In the high plains, the subspecies is absent or so rare that adequate quadrat samples are not available. In the better-watered highlands of New Mexico and Arizona it reemerges, however, but with such increased quadrat means that an effective mimicry of the introgressive populations of the Mississippi valley is obtained. Here also associated changes in other characters, especially greatly reduced width, produce something of a distinct racial facies.

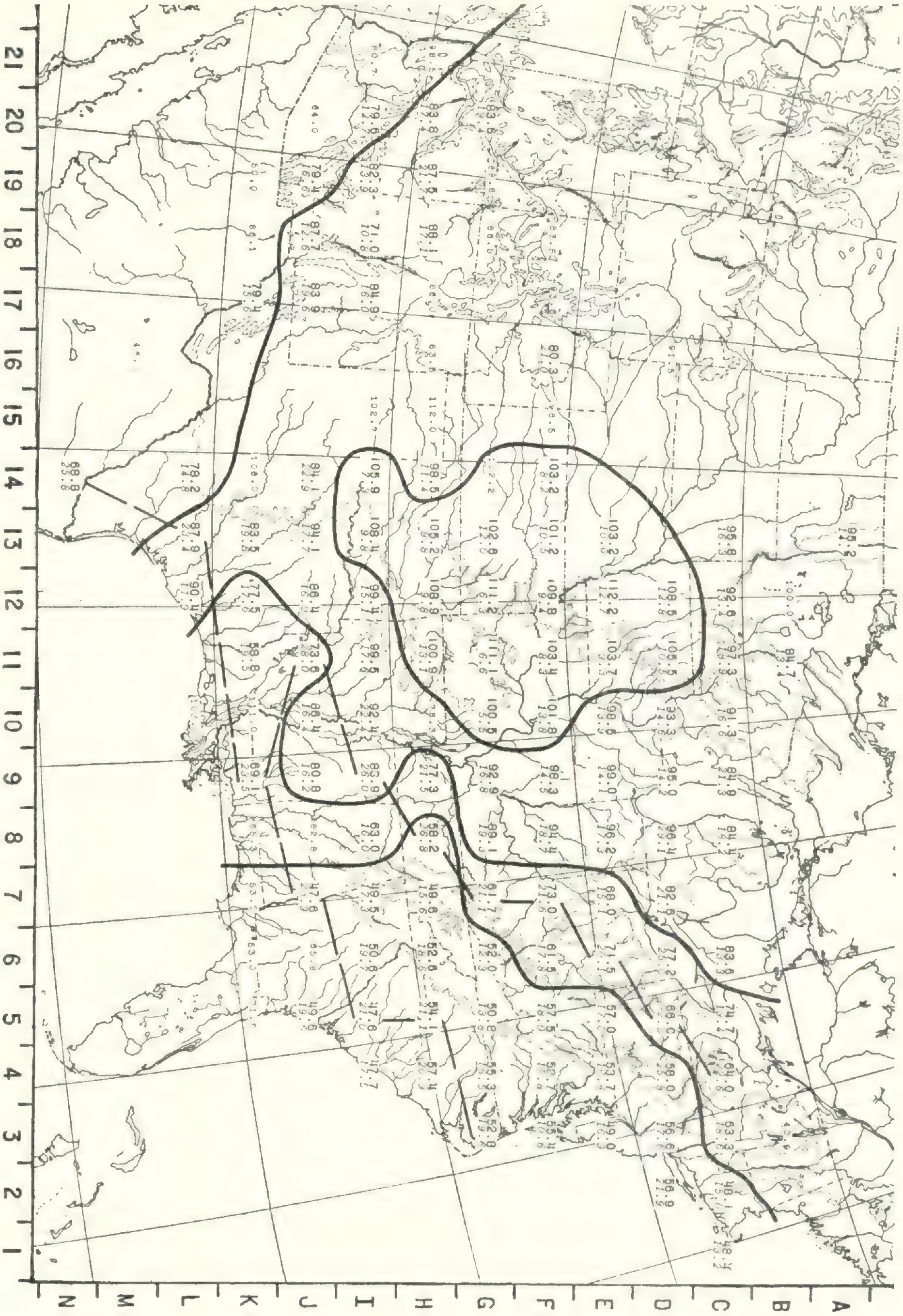
∠B

The phenocontour chart for ∠B, reproduced as Map IV, presents quadrat statistics in the same manner as did that for ∠A, but in this case isophenes have been drawn at intervals of 20° from the eastern seaboard. This interval was chosen after a hasty examination showed it to be the smallest which would produce continuous contours; hence it was surprising as well as gratifying when three isophenes emerged, separating four contours as in the preceding map. Here also the ranges of "true" *A. t. tuberosa* and "true" *A. t. interior* have much the previous relation to the Appalachian and Ozark plateaus, respectively, and the middle isophene denoting the midcurrent of introgression has somewhat the same course.

Dissimilarities to the ∠A map are striking, nevertheless. The isophenes themselves are more irregular and somewhat closer together, denoting a steeper cline. The eastern isophene, limiting the range of "true" ssp. *tuberosa*, has a more abrupt course to the Gulf coast, the reason for which will become apparent.

The phenocontours of ssp. *interior* are rather more complex than for ∠A, and show intra-subspecific differentiation in ∠B to be greater than in the former character. A far southwestern isophene is discovered here as well. Fortunately, confusion with the introgressive middle isophene is avoided here, since the two are not continuous. The most striking feature, however, is the irregularly elliptic 100°–110° contour eccentric in a northeasterly direction from the Ozark plateau.

The middle, introgressive, isophene is regular in the northern, glaciated states, and follows a course precisely similar to that seen in the map for ∠A. The southern half, however, is very irregular, showing three extensive and opposed embayments. Before interpreting these irregularities, we may observe that they



Map IV. *Asclepias tuberosa*: phenocontour system of ∠B (leaf base). Explanation in the text.

are the cause of the peculiarities of the ranges of the "true" subspecies already noted: the eccentricity of the 100°–110° contour of ssp. *interior*, and the abrupt course to the Gulf of the delimiting isophene of "true" ssp. *tuberosa*, or possibly the reverse is a more defensible position. At any rate, the evidence is mutually corroborative.

I would interpret the anomalous "bays" of the middle isophene as possibly connected with ecological, or at least floristic, selection. The Gulf coast embayment of the 60°–70° contour is a striking duplicate of typical southeastern coastal plain distributional extensions with which every plant geographer is thoroughly familiar. I believe that *A. t. Rolfsii* is implicated rather than *A. t. tuberosa* in this instance, because of the different characters of their distribution. Having been forced to omit the typical Floridian population from statistical analysis, this and another phenomenon to be presented shortly constitute our only evidence of the role of *Rolfsii* in introgression with the other subspecies.

The eastward embayment of the 80°–90° contour is typical, if less familiar, of the western floristic affinities of the isolated prairies of the middle-lower Mississippi valley (cf. Anderson & Woodson, 1935, in regard to *Tradescantia occidentalis* in eastern Arkansas). The third and northernmost embayment westward probably testifies to the Appalachian affinity of the area about the Nashville basin. The conclusion to be drawn from the embayments possibly is that in some way these floristic regions are peculiarly conducive to either subspecies as the case may be, and that in some way the factors for leaf base are correlated with others governing ecological adaptability of the subspecies in a manner not affecting leaf taper. With data as fragmentary as it is, the differential gene flow for the characters ∠A and ∠B in this region nonetheless appears obvious.

In discussing the map for ∠A, attention was called to the distinctive statistical facies of the quadrat populations. The same heterogeneity within continuity is found to obtain with regard to ∠B, although here it assumes more significant proportions. Attention was directed in the earlier discussion to the southwestern diversification of *A. t. interior*. Something of the same phenomenon is seen to involve ∠B. Here, intra-subspecific differentiation produces an irregularly centrifugal lowering of the quadrat ∠B means, i. e., a tendency for the leaves to become progressively less cordate. This phenomenon, together with others associated with it, will be examined more closely in another section of this study.

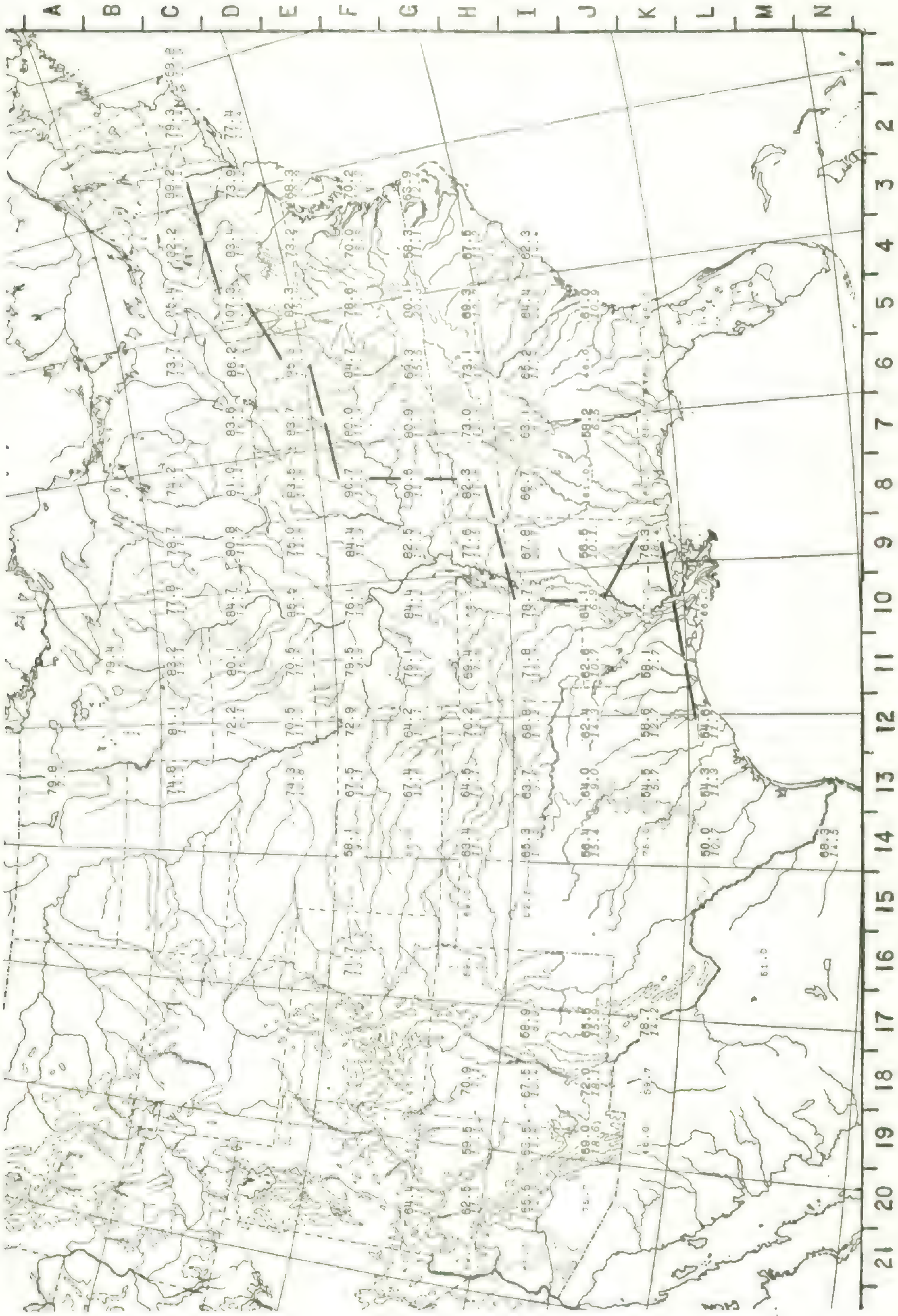
Perhaps the most striking feature of Map IV is the two convergent series of broken lines. These lines were drawn connecting quadrats having the greatest standard deviations when it was discovered that the deviations for ∠B means, unlike those for ∠A means, appear to have a more or less defined contour system of their own. The series of broken lines from central New York to Texas was drawn first, connecting the highest deviations in each horizontal rank of statistics. After this was completed, I observed that a similar, almost parallel, contour to the southeast could be obtained by connecting the deviations next in size.

As far as I am aware, this type of introgressive contour has not been discussed previously, and has not been provided with a name. I shall call it merely the "crest of variability" until I am inspired by appropriate classical roots. At any rate, involved with physiographic allegory as we are, it is natural to think of these crests of variability of ∠B as being due to a kind of genetic orogeny produced by introgression pressure from the three subspecies. This interpretation is supported by the obvious fact that the longer crest follows the 60°–70° contour between *A. t. tuberosa* and *A. t. interior* quite closely, and that the shorter crest to the southeast approximates the commissure of *A. t. tuberosa* and *A. t. Rolfsii* in almost exactly the position that any plant geographer would predict.

It would appear remarkable indeed if the longer crest of variability were to parallel more exactly the middle isophene throughout its devious southern course. Two explanations of its rather minor unconformity suggest themselves: one statistical, the other biological. The first concerns the strategic population in central Alabama which unfortunately contains too few cases for the computation of standard deviation. Were this statistic sufficiently large, the crest of variability would pass through it and successfully negotiate the sharp turn into coastal Texas in perfect harmony with the sinuous contour. The second explanation is less trifling: the fact that any increased variability due to heterozygosis must be superimposed upon the pre-existing parameter variability of each quadrat, the range of which may be seen by observing the heterogeneity of deviations in areas not possibly affected by introgression. The intriguing fact, therefore, is that the crest is as consistent as it is.

The relatively close conformity of the longer crest of variability with the 60°–70° contour leads me to conclude that introgression is progressing more rapidly from west to east, and threatens to engulf the Appalachian population. Evidence that *Rolfsii* is advancing in similar fashion will be deduced later. Caught between the advances of its sister subspecies upon either side, the ultimate reduction of ssp. *tuberosa* to a hybrid swarm would appear unavoidable. Some indications of the rate and manner in which this is being accomplished will follow shortly.

That no crest of variability was produced on the map for ∠A, such as that which we have just seen with regard to ∠B, appears of fundamental importance to me. I am led to the conclusion that very different gene actions must be responsible for the expression of the two characters. According to the theory of oligogenes and polygenes (Mather, 1942), one might expect such a crest of variability in introgressions involving the former and not the latter. The great difficulty in applying this theory to our phenocontour data is the lack of knowledge concerning the hereditary mechanism governing the characters measured. This is scarcely surprising since the plants do not lend themselves easily to breeding experiments, and further because both characters of leaf shape may be presumed to be controlled by multiple factors. A consequent difficulty for me is uncer-



Map V. *Asclepias tuberosa*: phenocontour system of median length of leaves. Explanation in the text.

tainty whether one should regard oligogenes and polygenes as allowing an ample continuous scale of graded expression; in other words, how many genes may constitute an oligogene complex, and how few a polygene, or is the distinction a relative one?

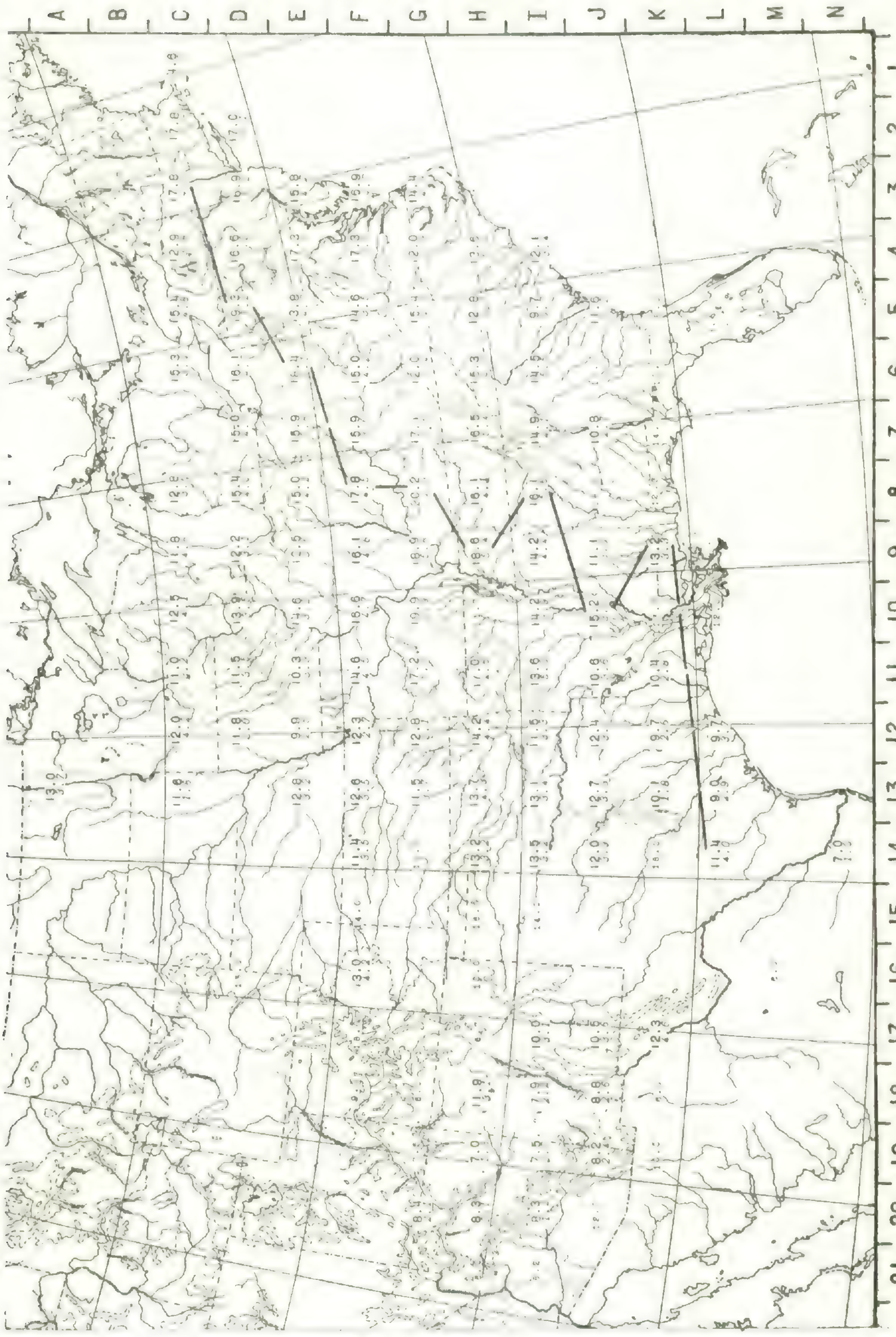
LENGTH AND WIDTH

The phenocontours of median length (Map V) and median width (Map VI) may be discussed together since they show much the same characteristics. In both maps the same tendency of quadrat populations to drift about individual means and variabilities is seen, as has been noted in connection with the other characters. In the maps for length and width, however, it is not practicable to draw isophenes, since these characters are not involved in the differentiation of the subspecies. In Map V an irregular tendency may be noted for leaves of both subspecies to be somewhat longer in the north than in the south. In Map VI the leaves of *A. t. interior* are found to be narrowest in the extreme southwest of the range. It seems most probable that these tendencies are produced in response to climate, from what we have learned of the relative frequency of the subspecies in different parts of its range; the result is a series of rather poorly defined ecoclines.

The most prominent feature of both maps is the oblique series of broken lines extending from New York state to coastal Texas. These lines, in both instances, connect the largest mean in each horizontal rank of quadrats, with the exclusion of the far southwestern quadrats of Map V. The two courses of broken lines are almost identical, diverging in respect to only two pairs of quadrats. It is apparent also that they approximate very closely the crest of variability observed with regard to $\angle$ B, even to the peculiar switch-back on the Gulf coast.

I cannot conceive, upon the evidence of the three maps, that the courses of broken lines for length and width can indicate other than hybrid vigor. Environmental effect can be discounted apparently because the lines run contrary to the ecocline contours for length. The combination of the two effects may be seen in both maps in that there is a general tendency for the maximum means to decrease from north to south. Of further interest is the indication that heterosis, if such it be, has little effect upon the variability of the populations with regard to length and width. These two properties would indicate that heterosis in natural populations, like the crest of variability previously discussed, is a quality superimposed upon previously established quadrate parameters. Heterosis cannot be regarded as greater in the northern states, and therefore that those populations are more heterozygous, simply because the northern maxima are greater than are those in the south. Northern leaves, *in general,* are larger than those in the south. This explains why the crests of length and width maxima do not correspond exactly, and, I am confident, why they do not correspond exactly with the crest of variability.

Several genetical problems of importance arise in reply to the interpretations which have just been made. Since a crest of variability was observed between the



Map VI. *Asclepias tuberosa*: phenocontour system of median width of leaves. Explanation in the text.

ranges of ssp. *tuberosa* and ssp. *Rolfsii*, why is there no parallel heterosis similar to that involving *tuberosa* and *interior*? One might suppose that the differences distinguishing the former two were insufficient to produce the necessary relational genic disbalance. From the purely systematic point of view, there can be little doubt that *tuberosa* and *Rolfsii* are more closely related than is either to *interior*. The difference between the two former, however, still must be sufficient to produce the crest of variability.

It is conceivable that *tuberosa* and *interior* have been in direct contact only since colonial times, due to the clearing of land, the building of roads, etc., although we can scarcely be sure of this. Even so, how has heterosis been maintained to the present day? Only by continuous gene flow from inbred populations, we may expect. Of importance in this regard, probably, are the air-borne seeds and peculiar adaptations to insect pollination described in the earlier portion of this paper.

Heterosis, according to Mather (1943) and others, results from the bringing together of polygenic combinations which have not been selected for good relational balance, and because of this, the phenotype of the hybrid will be likely to show a greater departure from the optimum than does either parent. It follows that heterosis is a sure sign of poor adaptation, and must be selectively disadvantageous and less "fit" than the parental types. In this way, it is believed, isolating mechanisms and hybrid sterility originate; indeed, "the avoidance of heterosis is the most widespread stimulant of isolating devices."

Certainly it would be unbecoming of me to enter into a controversy of genetical theory. In my opinion, however, there is a tendency to ascribe too uniform selective value to indiscriminate types of biological variations. Until a correlated character involving some aspect of viability or physiological efficiency is discovered, I can attach little selective advantage to any of the types of leaves which I have measured. I am convinced that plants of the inclusive species *Asclepias tuberosa* are nowhere as frequent, as fertile, nor as happily adapted to their environment as in the zig-zag commissure between the subspecies *tuberosa* and *interior*, where they apparently are most heterozygous.

With gradual discontinuance of out-breeding to "pure" types, I would expect relative subsidence of both excessive variability and heterosis, and a genetic peneplanation to a poorly differentiated hybrid swarm—the raw material of future speciation. In the light of our introductory discussion of paleogeography, I can see no reason why this has not occurred, perhaps repeatedly, in the past. A primary function of introgression may be the imparting of greater variability to specialized parental stocks. My experience in the field with the apparently successful establishment of introgressive populations of *A. tuberosa* prompts me to disbelieve that heterosis alone will lead to the erection of isolating devices to reseparate the subspecies. As a matter of fact, the following section of this study will produce evidence that introgression between *A. t. tuberosa*, *A. t. interior*, and *A. t. Rolfsii* is continuing apace.

V. Analysis of a Roadside Profile

In June, 1946, I made an automobile trip from Topeka, Kansas, to Norfolk, Virginia, accompanied by two of my friends, Richard W. Holm and George K. Richardson. The purpose of the journey was to collect leaves of butterflyweed from every colony of five or more plants encountered between those two points, for comparison with the herbarium data from a similar profile. The route chosen followed U. S. highway 40 eastward to St. Louis, U. S. 50 and 150 to Louisville, and U. S. 60 to Norfolk. The final collection, as a matter of fact, was made at Chuckatuck, Virginia, a village on U. S. highway 17, a few miles south of Norfolk. The whole transect totals a distance of about 1200 miles.

The massive plants and broad trusses of brilliant flowers render *Asclepias tuberosa* a conspicuous object from a distance of many yards, even when surrounded by undergrowth equalling or exceeding its height. Cruising at a speed averaging approximately 40 m. p. h., my companions and I had no difficulty whatsoever in detecting the species, I should guess, from a distance averaging at least one-tenth mile along either side of the highway. With three pairs of eyes vying for the first welcome sight of orange, I fancy that few plants escaped us.

With the cry of "Butterflyweed!", brakes would scream and out we we would spring to see whether the find consisted of a single plant or two, which we would neglect, or a colony of at least five. If the colony proved to be a large one, all hands would set to work, quickly selecting a portion for exclusive attention, and nimbly divesting one flowering stem of each plant of a single "random" median leaf. Back in the car, the leaves would be united into a paper envelope inscribed with appropriate data, inserted into a press, and probably sat upon by Dick, George, or myself. Perhaps more important biometric material has been secured within four days, and from a wider area, but never more happily.

The transect which has just been described yielded a total of 994 leaves for measurement; these were distributed amongst 53 colonies of five plants or more. The largest colony numbered 77 plants; the median colony size for the whole transect was 13. Unfortunately, no record was kept of single plants encountered, nor of small colonies of less than five plants, but these certainly were met with far more seldom than the "larger" colonies; perhaps a total of 1050 plants were encountered in all.

The distance between colonies for which records were kept varied from 3 to 107 miles, with a median distance of 12 miles. Between these, of course, were interspersed the single plants and smaller colonies. The mean distance between colonies varied in a manner to which some degree of significance may be attached, the greatest concentration occurring in Kansas and Missouri (16–22 miles) on the western end, and Virginia (14 miles) on the eastern. The most sparse colonies were encountered in Illinois, where the mean distance was 46 miles. From such a small sampling, only a general inference may be made to the effect that the colonies

were more frequent the closer to the putative centers of origin of the two subspecies, an observation which I take to have more paleogeographic than genetical bearing.

As relief from more practical considerations, I have indulged in some conjecture concerning the total population of *Asclepias tuberosa* in the United States. From the details of the journey which have been given, it may be estimated crudely that a total area approximating 243.6 square miles was searched for butterflyweed, with an estimated total of 1050 plants, yielding a density approximately of 4.3 per square mile. Estimating the total area of the species as 1,434,000 square miles, a total population in excess of 6,000,000 plants is suggested. The unreliability of this figure is emphasized by the realization that the area actually sampled equals less than one-five thousandths of the estimated total area!

Similarly facile computations may be made concerning the potential fecundity of the species for comparison with the estimated frequency which has been observed. For our crude purposes, we may assume the potential fecundity of an "average" plant of butterflyweed to be the product of approximately 100 ovules distributed amongst 2 carpels for each of 18 flowers per cyme, with 15 cymes per stem. Assuming an average of 15 stems per plant, a potential seed crop of 405,000 seeds per plant is indicated, a figure which is no more disproportionate to actual population than is usual in such computations.

In the earlier discussion of the biology of the species, certain mechanical factors influencing the failure to realize this potential fecundity have been indicated, *i. e.*, difficulties of pollen transference and the division of the stigmatic surface into 5 separate areas. To these must be added the observed somatoplastic sterility and relatively low germination in nature, as well as the more enigmatic animal predators and rigors of ecological competition. Having by no means exhausted the possibilities, it is clear why plants are such satisfactory subjects for systematic and geographical studies: why they stay "close to home" as a rule; why they are conservative to evolutionary change. It also is clear why more precise genetic concepts are not forthcoming from studies such as these.

Table IV presents the individual statistics for the 53 colonies of butterflyweed encountered along the 1218-mile profile from Topeka, Kansas, to Chuckatuck, Virginia. In fig. 4 they are presented in the form of a composite graph, including the means and standard deviations for the four characters of ∠A, ∠B, median length, and median width. The abscissa of the graph indicates the proportionate distances of the colonies, the numbers corresponding to those employed in Table IV. The principal physiographic features encountered in the transect are indicated on the face of the graph between the data for length and width. Drawn to such a scale, the clines and other features noted in the phenocontour maps are scarcely recognizable in fig. 4, which to this degree approaches reality rather disconcertingly. Nevertheless, with a bit of scrutiny, the graphs may be found to corroborate satisfactorily the clines, as well as the crests of variability and hybrid vigor to which attention was called by the maps.

TABLE IV

MEASUREMENTS OF LEAVES OF *ASCLEPIAS TUBEROSA* (SENSU LAT.) ASSEMBLED ACCORDING TO NATURAL COLONIES ALONG ROADSIDES FROM TOPEKA, KANSAS, TO CHUCKATUCK, VIRGINIA

(Means, standard errors, standard deviations, and coefficients of variation; angles in degrees, length and width in millimeters)

No.	Colonies		∠A			∠B			Length			Width		
	Location	N	$\bar{X}$	s	V	$\bar{X}$	s	V	$\bar{X}$	s	V	$\bar{X}$	s	V
1	East of Topeka, Shawnee Co., Kans.	11	84.6 ± 0.6	2.0	2.4	106.3 ± 1.9	6.2	5.8	63.4 ± 2.8	8.8	13.9	12.4 ± 1.1	3.4	27.4
2	8 mi. east of Topeka, Shawnee Co., Kans.	10	85.0 ± 0.2	0.7	0.8	104.2 ± 2.8	8.5	8.1	67.2 ± 2.1	6.3	9.4	12.8 ± 0.4	1.3	10.1
3	West of Lawrence, Douglas Co., Kans.	15	84.5 ± 0.4	1.3	1.5	110.6 ± 2.4	8.9	8.0	72.3 ± 3.3	12.3	17.0	14.3 ± 1.9	4.1	28.6
4	Lawrence, Douglas Co., Kans.	33	84.7 ± 0.2	1.4	1.7	107.3 ± 1.2	6.6	6.2	73.2 ± 2.0	11.1	15.2	14.4 ± 0.6	3.3	22.9
5	10 mi. east of Lawrence, Douglas Co., Kans.	17	85.3 ± 0.2	1.7	1.8	107.5 ± 1.8	7.3	6.8	69.6 ± 2.8	11.2	16.1	14.1 ± 0.7	2.7	19.1
6	20 mi. east of Kansas City, Jackson Co., Mo.	10	86.0 ± 0.4	1.2	1.4	113.3 ± 1.6	4.7	4.1	71.9 ± 5.0	14.9	20.7	13.8 ± 0.5	1.6	11.6
7	East of Odessa, Lafayette Co., Mo.	10	87.0 ± 0.3	0.9	1.0	101.5 ± 2.4	7.3	7.2	79.3 ± 3.4	10.1	12.7	13.0 ± 2.5	2.8	21.5
8	6 mi. west of Concordia, Lafayette Co., Mo.	8	85.3 ± 0.5	1.2	1.4	99.6 ± 3.9	10.3	10.3	84.1 ± 3.9	10.2	12.1	14.6 ± 1.2	3.1	21.2
9	Southwest of Marshall, Saline Co., Mo.	7	85.8 ± 0.9	2.2	2.6	107.8 ± 5.8	17.8	22.0	81.0 ± 7.3	17.8	22.0	16.6 ± 2.1	5.1	30.7
10	East of Columbia, Boone Co., Mo.	11	85.9 ± 0.5	1.6	1.6	108.2 ± 3.7	11.6	10.5	87.2 ± 2.8	8.9	10.2	17.8 ± 1.2	3.9	21.9
11	2 mi. east of Kingdom City, Callaway Co., Mo.	5	85.8 ± 1.5	3.0	3.5	105.7 ± 4.1	8.2	7.8	76.2 ± 5.4	10.7	14.0	18.0 ± 2.6	5.2	28.9
12	4 mi. east of Kingdom City, Callaway Co., Mo.	17	85.9 ± 0.3	1.1	1.5	96.1 ± 2.2	8.8	9.2	85.2 ± 1.6	6.5	7.6	17.6 ± 1.1	4.2	23.5
13	Warren-Montgomery county line, Mo.	5	89.2 ± 1.1	2.1	2.4	85.5 ± 8.8	17.5	20.5	73.8 ± 4.6	9.1	12.3	13.0 ± 0.7	1.4	10.8
14	2 mi. east of Wright City, Warren Co., Mo.	11	87.3 ± 0.4	1.3	1.4	92.9 ± 3.9	12.4	13.4	73.9 ± 3.0	9.5	12.8	16.1 ± 1.5	4.6	28.6

TABLE IV *(Continued)*

No.	Colonies		∠A			∠B			Length			Width		
	Location	N	$\bar{X}$	s	V	$\bar{X}$	s	V	$\bar{X}$	s	V	$\bar{X}$	s	V
15	Wentzville, St. Charles Co., Mo.	32	87.1 ± 0.2	0.9	1.0	97.7 ± 1.7	9.4	9.6	85.4 ± 2.6	14.6	17.1	15.9 ± 0.6	3.5	22.1
16	Glendale, St. Louis Co., Mo.	36	86.6 ± 0.3	1.5	1.7	97.3 ± 2.2	13.2	13.6	86.2 ± 2.1	12.1	14.0	18.1 ± 0.9	5.2	28.7
17	Edwardsville, Madison Co., Ill.	20	87.6 ± 0.2	1.0	1.1	108.4 ± 2.3	10.1	9.3	83.7 ± 1.1	5.0	5.9	15.6 ± 0.8	3.3	21.2
18	West of Trenton, Clinton Co., Ill.	8	87.1 ± 0.3	0.9	1.0	100.6 ± 3.0	8.0	7.9	80.4 ± 5.3	14.1	17.5	15.4 ± 0.6	1.7	11.0
19	East of Bridgport, Lawrence Co., Ill.	5	89.0 ± 0.8	1.6	1.8	92.1 ± 10.1	20.2	21.9	77.2 ± 2.1	8.4	10.9	14.4 ± 1.4	2.9	20.1
20	Washington, Daviess Co., Ind.	5	86.2 ± 1.2	2.4	2.8	96.5 ± 2.7	5.5	5.7	93.2 ± 5.0	10.0	10.7	21.4 ± 1.8	3.5	16.4
21	East of Washington, Daviess Co., Ind.	13	88.3 ± 0.4	1.5	1.7	89.2 ± 2.5	9.5	10.6	104.9 ± 4.6	15.9	15.2	21.4 ± 1.0	3.4	15.9
22	Southeast of Paoli, Orange Co., Ind.	77	89.1 ± 0.2	1.2	1.4	79.8 ± 1.8	16.0	20.0	92.5 ± 1.5	12.2	13.2	16.9 ± 0.4	3.4	20.1
23	East of Shelbyville, Shelby Co., Ky.	46	88.9 ± 0.2	1.5	1.7	75.0 ± 2.9	19.8	26.4	92.2 ± 1.9	12.6	13.7	20.6 ± 0.7	4.7	22.8
24	East of Owingsville, Bath Co., Ky.	17	89.6 ± 0.2	1.0	1.1	61.1 ± 4.5	18.0	29.5	93.4 ± 2.7	10.7	11.5	17.5 ± 0.6	2.6	14.9
25	Northeast of Morehead, Rowan Co., Ky.	6	89.1 ± 0.5	1.2	1.3	52.8 ± 4.4	9.8	18.6	99.0 ± 3.9	8.7	8.8	18.3 ± 1.5	3.4	18.6
26	Eadston, Rowan Co., Ky.	12	89.8 ± 0.4	1.2	1.3	68.0 ± 5.2	17.4	25.2	110.9 ± 3.7	12.2	11.0	15.1 ± 1.2	4.1	27.1
27	Grayson, Carter Co., Ky.	6	90.2 ± 0.4	0.8	0.9	49.6 ± 2.0	4.5	9.1	81.3 ± 11.6	26.1	32.1	12.8 ± 2.2	5.0	39.1
28	Jaffie, Lawrence Co., Ky.	5	89.0 ± 0.6	1.1	1.2	70.4 ± 3.4	6.7	9.5	103.2 ± 1.6	3.3	3.2	23.6 ± 1.9	3.9	14.8
29	East of Huntington, Cabell Co., W. Va.	8	90.0 ± 0.4	1.1	1.2	68.1 ± 6.7	17.8	26.2	97.9 ± 4.2	17.8	11.3	15.5 ± 1.2	3.3	21.3
30	Milton, Cabell Co., W. Va.	8	90.4 ± 0.4	1.1	1.2	47.6 ± 4.5	12.0	25.2	90.2 ± 4.5	12.0	13.3	15.3 ± 2.0	5.2	33.9

TABLE IV *(Continued)*

No.	Colonies		∠A			∠B			Length			Width		
	Location	N	$\bar{X}$	s	V	$\bar{X}$	s	V	$\bar{X}$	s	V	$\bar{X}$	s	V
31	East of Milton, Cabell Co., W. Va.	11	87.8 ± 0.7	2.3	2.6	70.3 ± 5.8	18.2	25.9	103.7 ± 7.6	24.0	23.1	20.1 ± 1.3	4.0	19.9
32	Gauley's Mountain, Fayette Co., W. Va.	17	89.6 ± 0.4	1.6	1.8	55.6 ± 3.4	13.5	24.3	89.7 ± 3.4	13.8	15.4	14.0 ± 0.7	2.8	20.0
33	West of Covington, Allegheny Co., Va.	11	88.7 ± 0.4	1.5	1.7	67.7 ± 4.8	15.1	22.3	73.7 ± 2.7	8.7	11.8	16.8 ± 1.0	3.2	19.0
34	Covington, Allegheny Co., Va.	60	88.1 ± 0.2	1.8	2.0	70.3 ± 2.4	18.2	25.9	71.2 ± 1.8	13.7	19.2	16.7 ± 0.6	4.8	28.7
35	North Mountain, Rockbridge Co., Va.	67	89.1 ± 0.2	1.7	1.9	76.4 ± 2.2	17.7	23.2	85.3 ± 1.4	11.8	13.8	18.4 ± 0.6	5.2	28.3
36	North Mountain, Rockbridge Co., Va. (2nd colony)	21	89.4 ± 0.4	1.6	1.8	64.1 ± 3.7	16.6	25.9	75.9 ± 2.6	11.6	15.3	16.3 ± 1.2	5.2	31.9
37	East slope, North Mountain, Rockbridge Co., Va.	8	90.4 ± 0.7	1.8	2.0	68.3 ± 8.1	21.6	31.6	89.1 ± 5.5	14.4	16.2	15.8 ± 1.1	2.9	18.4
38	East of Lexington, Rockbridge Co., Va.	53	89.9 ± 0.2	1.4	1.6	70.0 ± 2.4	17.6	25.1	80.9 ± 1.7	12.4	15.3	19.9 ± 0.7	4.8	24.1
39	West of Amherst, Amherst Co., Va.	26	89.3 ± 0.4	2.1	2.4	63.9 ± 3.8	19.0	29.7	83.7 ± 2.8	14.1	16.8	23.3 ± 1.2	5.8	24.9
40	Bent Creek, Appomattox Co., Va.	6	88.8 ± 0.6	1.4	1.6	69.8 ± 4.3	9.5	13.6	88.8 ± 6.2	13.9	15.7	25.7 ± 1.9	4.2	16.3
41	Between Bent Creek and Buckingham, B'ham Co., Va.	14	89.9 ± 0.4	1.6	1.8	64.5 ± 5.1	18.3	28.4	67.8 ± 2.9	10.6	15.6	18.7 ± 2.0	7.2	38.5
42	Buckingham, Buckingham Co., Va.	34	90.5 ± 0.3	1.7	1.9	66.5 ± 2.8	15.8	23.8	72.7 ± 2.1	12.3	16.9	19.3 ± 0.8	4.0	20.7
43	8 mi. west of Cumberland, Cumberland Co., Va.	5	87.9 ± 1.8	3.6	4.3	64.9 ± 6.6	13.3	20.5	79.6 ± 6.8	13.7	17.2	22.2 ± 4.0	8.1	36.5
44	Northwest of Skinquarter, Powhatan Co., Va.	20	89.9 ± 0.4	1.6	1.8	71.8 ± 3.1	13.3	18.5	66.7 ± 2.9	12.4	18.6	17.0 ± 1.0	4.2	24.7
45	Midlothian, Chesterfield Co., Va.	15	90.7 ± 0.4	1.6	1.8	76.4 ± 3.4	12.8	16.8	63.4 ± 3.2	11.8	18.6	16.1 ± 1.0	3.8	23.6

TABLE IV *(Continued)*

No.	Colonies		∠A			∠B			Length			Width		
	Location	N	$\bar{X}$	s	V	$\bar{X}$	s	V	$\bar{X}$	s	V	$\bar{X}$	s	V
46	Providence Forge, New Kent Co., Va.	13	91.6 ± 0.6	2.0	2.2	61.5 ± 4.1	14.2	23.1	62.4 ± 3.1	10.7	17.1	14.2 ± 0.9	3.0	21.1
47	Providence Forge, New Kent Co., Va. (2nd colony)	7	88.7 ± 0.7	1.7	1.9	69.8 ± 7.2	17.7	25.4	65.3 ± 3.1	7.7	11.8	16.3 ± 1.3	3.3	20.2
48	Windsor Shades, New Kent Co., Va.	44	89.0 ± 0.3	2.2	2.5	74.1 ± 2.1	13.8	18.6	70.6 ± 1.8	11.6	16.4	19.1 ± 0.8	5.6	29.3
49	West of Toano, James City Co., Va.	17	90.1 ± 0.6	2.2	2.4	70.3 ± 3.5	13.9	19.8	66.8 ± 2.8	11.3	16.9	14.9 ± 0.9	3.7	24.8
50	Ewell, James City Co., Va.	6	89.6 ± 0.6	1.4	1.6	70.5 ± 6.1	13.5	19.1	68.2 ± 3.5	7.9	10.1	16.5 ± 1.8	4.0	24.3
51	Lee Hall, Warwick Co., Va.	20	91.6 ± 0.4	1.6	1.7	57.8 ± 4.4	19.0	32.9	69.2 ± 1.7	7.4	10.8	16.6 ± 0.8	3.3	19.9
52	Benn's Church, Isle of Wight Co., Va.	31	91.1 ± 0.3	1.4	1.5	56.4 ± 2.3	12.4	22.0	69.1 ± 2.2	12.2	17.7	18.5 ± 1.0	5.6	30.3
53	South of Chuckatuck, Nansemond Co., Va.	14	92.1 ± 0.4	1.2	1.3	54.5 ± 2.5	9.0	16.5	75.3 ± 3.2	11.4	15.1	14.7 ± 1.0	3.6	24.5

Aside from area, the first feature of the graph to catch the eye may be the relative smoothness of the curves for width, and particularly for ∠A, in contrast to those for ∠B and length. This is chiefly a statistical effect occasioned by the small total range of ∠A means, on the one hand, and the relatively small size of width means, on the other. If *V* had been used as a standard measure of variability instead of *s*, for example, the curve for width would have been the most irregular by far.

A more significant feature is seen in the increased irregularity of all curves from the Allegheny Mountains eastward to the coast. Since the profile traverses the central lowlands westward to the Alleghenies, an accounting factor for the conspicuous variability eastward might be advanced as the more varied topography *per se*. Considering the roadside origin of my samples, I am not impressed by this explanation. Another might be the assumption of greater intrinsic variability in colonies of *A. t. tuberosa* than in those of *A. t. interior*. This is not likely since certain colonies of the former on the Atlantic seaboard have quite as low variability as colonies of the latter on the midwestern plains.

I am disposed to view the regularity west of the Alleghenies and the irregularity to the east as being evidence of greater migration pressure of the western subspecies, producing greater heterozygosity, and hence variability, in the eastern population through introgression. I shall explore this possibility more fully in succeeding sections.

It is apparent that the colonies behave as microgeographic races, those immediately adjacent to one another often being more different, in a given character, than others a hundred or more miles away (cf. Anderson, 1936; Dice, 1940). Nevertheless, for all their haphazard courses, there are definite clines, both for ∠A and for ∠B. This composite effect presumably is the result of random fixation and loss of genes in colonies with limited effective population size (Dobzhansky, 1941), combined with the occasional exchange of genes between adjacent colonies. The latter, of course, is effected through insect agency in the final analysis, but doubtless is facilitated by the long-distance transport of seeds from either direction, particularly from west to east—the course of the prevailing winds.

In view of the relatively great distances between colonies, their relatively few individuals, and their distinctive parameters, I am of the opinion that such colonies are the progeny of a single plant germinating from a single wind-borne seed, as a rule; which in turn largely accounts for their distinctive facies. In consideration of the apparently facultative cross- or self-pollination, I assume the effective population size of butterflyweed to be low indeed.

A pair of little scatter diagrams which interest me specially are reproduced as figs. 5-6, since they do much to explain the genetic mechanism of introgression with regard to both ∠A and ∠B. In fig. 5, the dots represent the coincidence of the means of ∠A and ∠B obtained from each of the 53 colonies of butterflyweed

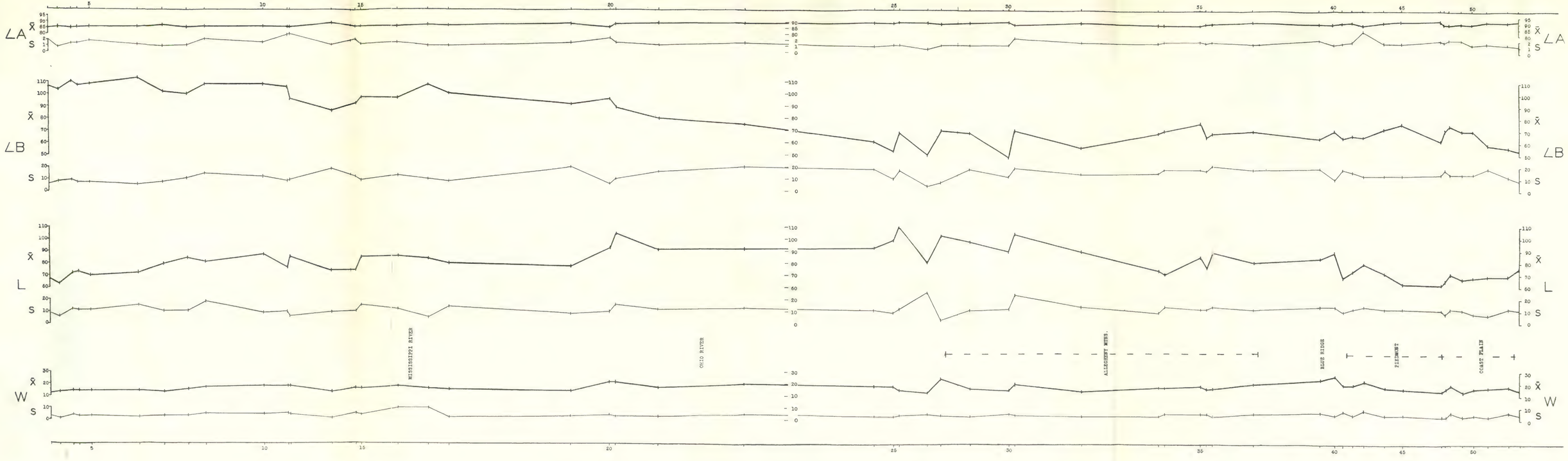


Fig. 4. Means and standard deviations of 53 colonies of butterflyweed along a roadside profile from eastern Kansas to Tidewater Virginia. Explanation in the text.

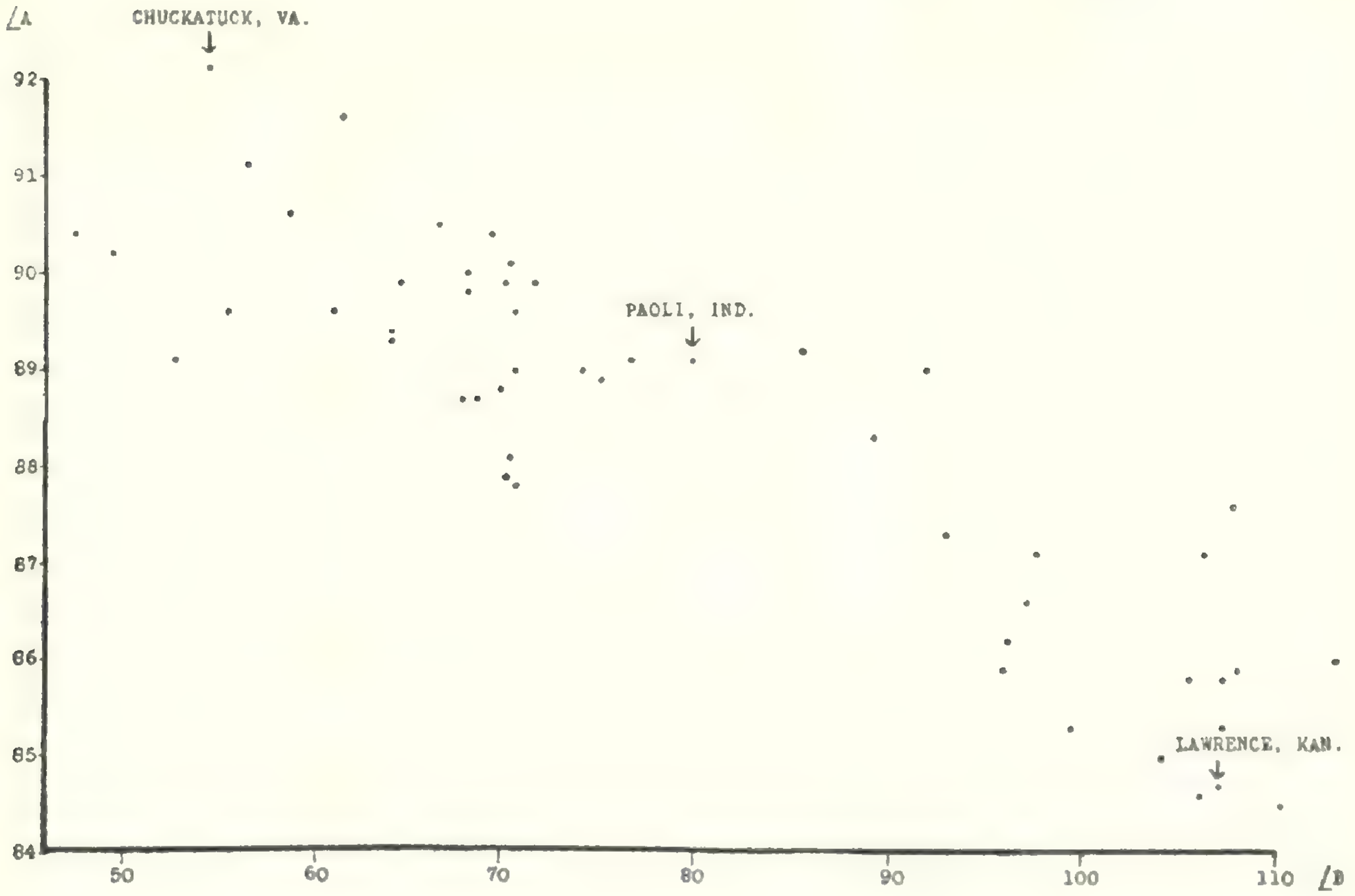


Fig. 5. Coincidence of colonial means for ∠A and ∠B along a roadside profile from eastern Kansas to the coast of Virginia. Explanation in the text.

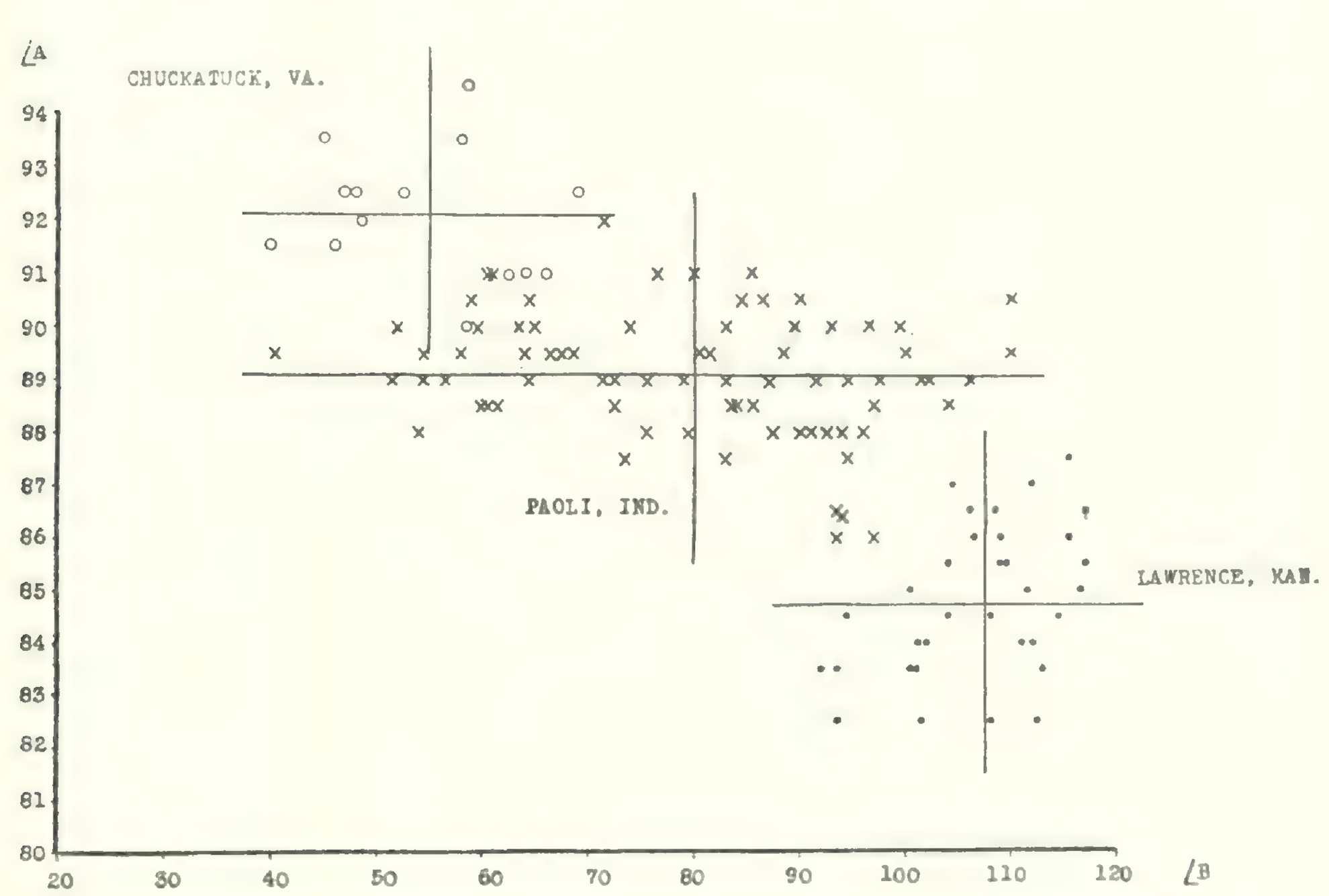


Fig. 6. Relation of ∠A and ∠B values in three colonies of butterflyweed. Explanation in the text.

extending from Topeka, Kansas, to Chuckatuck, Virginia. The close relation of intergrading phenotypes to geographical distribution appears striking, particularly with reference to the intergradation of high ∠A and low ∠B values at the eastern end, and low ∠A and high ∠B values in the west. The three colonies specially identified were chosen not only because they occur at both ends and middle of the distribution, but because their combined means represent satisfactorily the typical parameters of both subspecies and their cline, including sufficient cases for further analysis as well.

In fig. 6, the individual cases for Chuckatuck, Paoli, and Lawrence are superimposed upon the same grid, the three cross-bars indicating the respective coincidences of the means for ∠A and ∠B. The almost perfect confluence of the individual phenotypes of the three colonies, located almost equidistantly along the profile of nearly 1200 miles, is most satisfying.

Quantitative characters, notably leaf shape, usually have been found due to multiple factors exhibiting Mendelian segregation. That such is the case with respect to both ∠A and ∠B in butterflyweed leaves is suggested most forcibly by fig. 6, in which the Paoli colony assumes the properties of an experimentally produced F_2 between the Chuckatuck and the Lawrence populations. The range of ∠B of the former clearly more than equals the combined ranges of the latter two colonies. With respect to ∠A the situation is not so clear, since, although the range of Paoli is greater than that for either Chuckatuck or Lawrence, it is not equal to the combined ranges of the two latter. This, following Muller (1936), would indicate not the absence of multiple genes, but cancellation of variability in the F_2 by the intra-racial variation of the parent strains.

An additional inference to be gleaned from fig. 6 is the apparent absence at least of strong linkage between the genotypes of ∠A and ∠B for both Chuckatuck and Lawrence. In the Paoli colony, however, there is a slight tendency for the association of high ∠A and low ∠B expression, and *vice versa*. I assume this may indicate that the multiple gene complex governing either character is of a relatively high order, and that the genes may be distributed upon several chromosomes, or at least at several loci.

In view of our interpretations of figs. 5-6, it seems clear to me that the constellation of means presented in fig. 5 most probably is the result of the early hybridization of plants of *A. t. tuberosa* and *A. t. interior* at the initial juncture of their ranges, with successive back-crosses to other heterozygotes and the ancestral types producing the remarkably even clines with which we have become familiar. From the inferences which I have made concerning the complexity and distribution of the genotypes, I would expect a high chiasma frequency and abundant crossing-over to catalyze the process which we have been discussing. Equilibrium of the genic diffusion may conceivably be upset by such factors as the erection of sterility barriers, as Mather has suggested, but more particularly by

preponderant selection and migration pressure from one or the other of the introgressing populations, an example of which will be provided in a following section of this study.

COMPARISON OF THE HERBARIUM AND ROADSIDE PROFILES

It happens that the roadside profile just discussed falls for virtually its entirety within the horizontal rank of herbarium quadrats from *F3* to *F12* of the phenocontour maps. A comparison of the two sources of data presents some rather interesting topics for conjecture, and is documented graphically in fig. 7. Herbarium data have been borrowed from Table III; in Table V the roadside data from Table IV have been partitioned according to geographical provenience into a complementary series of quadrat populations which are numbered from *3* to *12* and preceded by the initial *Q*. It is essential, in the discussion which follows, for the reader to understand what I consider to be the important properties of these two samplings.

In the first place, I consider the herbarium data to be the most "normal" information available for the population of *Asclepias tuberosa* as it exists throughout its entire range, for reasons concerning the conditions of their collection which I have discussed previously. I believe that my arguments are substantiated sufficiently by the relatively consistent contours of the maps. The data, as far as the element of place is concerned, represent not one special type of habitat, but the sum-total of all types of environments which have been visited by the innumerable participating plant collectors. As far as the element of time is concerned, the properties of the herbarium data are more abstruse. They all have been collected during the blooming seasons of the plants, but during years as long ago as 1820 and as recent as 1946. A little research upon our collections in the herbarium of the Missouri Botanical Garden reveals that the majority of our specimens were prepared between the years 1890 and 1918. The plants, therefore, can only be said to represent, on the whole, the "recent past."

On the other hand, the roadside data are biased in two very important respects: they have been collected only along main-travelled highways, and only during the early summer of the year 1946. The essence of our contrast, therefore, consists of these two particulars: a "normal" collection, with regard to place, versus a roadside sample; and a collection made in the "recent past," versus a collection made during the year 1946. The latter, of course, is unsatisfactorily vague, but it is the best that can be done at the moment, and may be of some use. Should a collection of butterflyweeds be made for comparison twenty-five or fifty years from now along the route of my roadside profile, measured and treated in the same way, I expect that some interesting facts concerning evolutionary topics may be forthcoming.

Considering the small size of the two samplings, only 117 cases for the herbarium profile of over 1200 miles and 994 cases for the roadside, the first impression of fig. 7 may be the relative agreement of the two sets of curves. A second feature,

TABLE V

DATA FROM TABLE IV REASSEMBLED INTO EQUAL-AREA QUADRATS EQUIVALENT TO THOSE OF TABLE III

(Means, standard errors, standard deviations, and coefficients of variation; angles in degrees, length and width in millimeters)

		∠A			∠B			Length			Width		
Quadrat	N	$\bar{X}$	s	V	$\bar{X}$	s	V	$\bar{X}$	s	V	$\bar{X}$	s	V
Q3	152	90.4 ± 0.2	2.1	2.3	64.7 ± 1.3	16.3	25.2	69.1 ± 0.9	11.0	15.9	17.1 ± 0.4	5.0	29.2
Q4	120	89.9 ± 0.2	2.0	2.2	68.1 ± 1.4	15.7	21.6	73.0 ± 1.3	14.6	20.0	19.8 ± 0.5	5.7	28.8
Q5	237	89.1 ± 0.1	1.8	2.0	68.1 ± 1.2	17.8	26.0	79.4 ± 0.9	13.9	17.5	18.1 ± 0.3	5.0	27.6
Q6	32	89.2 ± 0.3	1.9	2.1	64.1 ± 3.2	17.7	27.6	98.8 ± 3.0	16.7	16.9	18.3 ± 0.9	5.2	28.4
Q7	87	89.3 ± 0.1	1.3	1.5	66.7 ± 2.1	19.5	29.2	94.6 ± 1.6	15.0	15.9	18.5 ± 0.5	4.8	25.9
Q8	95	88.8 ± 0.2	1.5	1.7	81.9 ± 1.6	15.7	19.2	94.2 ± 1.4	13.3	14.1	17.8 ± 0.4	3.8	21.4
Q9	13	87.8 ± 0.4	1.5	1.7	97.3 ± 4.0	13.8	14.3	79.1 ± 3.8	13.2	16.7	15.0 ± 0.6	2.2	14.7
Q10	104	87.1 ± 0.1	1.3	1.5	98.4 ± 1.2	12.7	12.9	83.6 ± 1.3	12.8	15.3	16.5 ± 0.4	4.2	25.4
Q11	58	86.0 ± 0.2	1.6	1.9	102.1 ± 1.4	10.8	10.6	83.1 ± 1.4	10.5	12.6	16.3 ± 0.6	4.2	25.8
Q12	96	84.9 ± 0.1	1.4	1.6	108.0 ± 0.8	7.5	6.9	70.5 ± 0.8	7.5	10.6	13.8 ± 0.3	3.1	22.5

which I may not have to point out, is that where there are disagreements of considerable degree, the discrepancies are consistent. These two properties are concomitant, and justify the acceptance of the two sources of data in contrasting their two properties of place and time.

∠A

Herbarium and roadside curves for both the means and standard deviations are very similar, but the curve for the roadside means is much smoother than is that for the herbarium. The consistency of the stepped aspect of the herbarium curve, in my opinion, argues against its interpretation as a statistical artifact, and that introgressive diffusion is unquestionably farther advanced along the roadside. Although the interval range of the *s* curves is almost too close for critical comparison, it will be seen that roughly the eastern half of the roadside profile is more variable than the western half. There is no crest of variability in either the roadside or the herbarium profile.

∠B

The ∠B curves for the means and the standard deviations for herbarium and roadside are more contrasting because of the wider interval ranges. It is seen that west of the Allegheny Mountains (quadrats *12* to *7*) the roadside populations have become somewhat more like the eastern subspecies; that of quadrat *8* (southern Indiana) strikingly so. From the Alleghenies to the Atlantic coast, however, the leaves of the roadside populations have shifted to a conspicuously higher ∠B, indicative of a leaf base more nearly approaching that of the western subspecies. The *s* curves are rather similar, but it probably is significant that variability of the roadside populations west of the Alleghenies has decreased, as a rule, whereas that to the east has been maintained or increased. This is consistent with our interpretation of the curves for ∠A.

LENGTH AND WIDTH

In interpreting the roadside and herbarium profiles, it should be remembered that it was found impossible, in dealing with the phenocontour maps, to plot isophenes for length and width. This apparently was due to the greater genetic drift of those characters in microgeographic races, but chiefly to the fact that the subspecies themselves are not differentiated by size factors.

Consequently, neither are our herbarium and roadside curves for length and width as easy of comparison as are those for ∠A and ∠B. In this case, the difficulty is accentuated because the data for the roadside are composed of relatively few specific colonies (or microgeographic races) which are particularly haphazard in the characters under consideration. Nevertheless, it will be seen that heterosis is suggested by the consistently larger leaves roughly from eastern Kentucky to the Atlantic seaboard, having apparently moved eastward together with the crest of variability of ∠B, as we might expect. The variability in length and width, rather oddly, has not increased notably; rather, the roadside curves have smoothed.

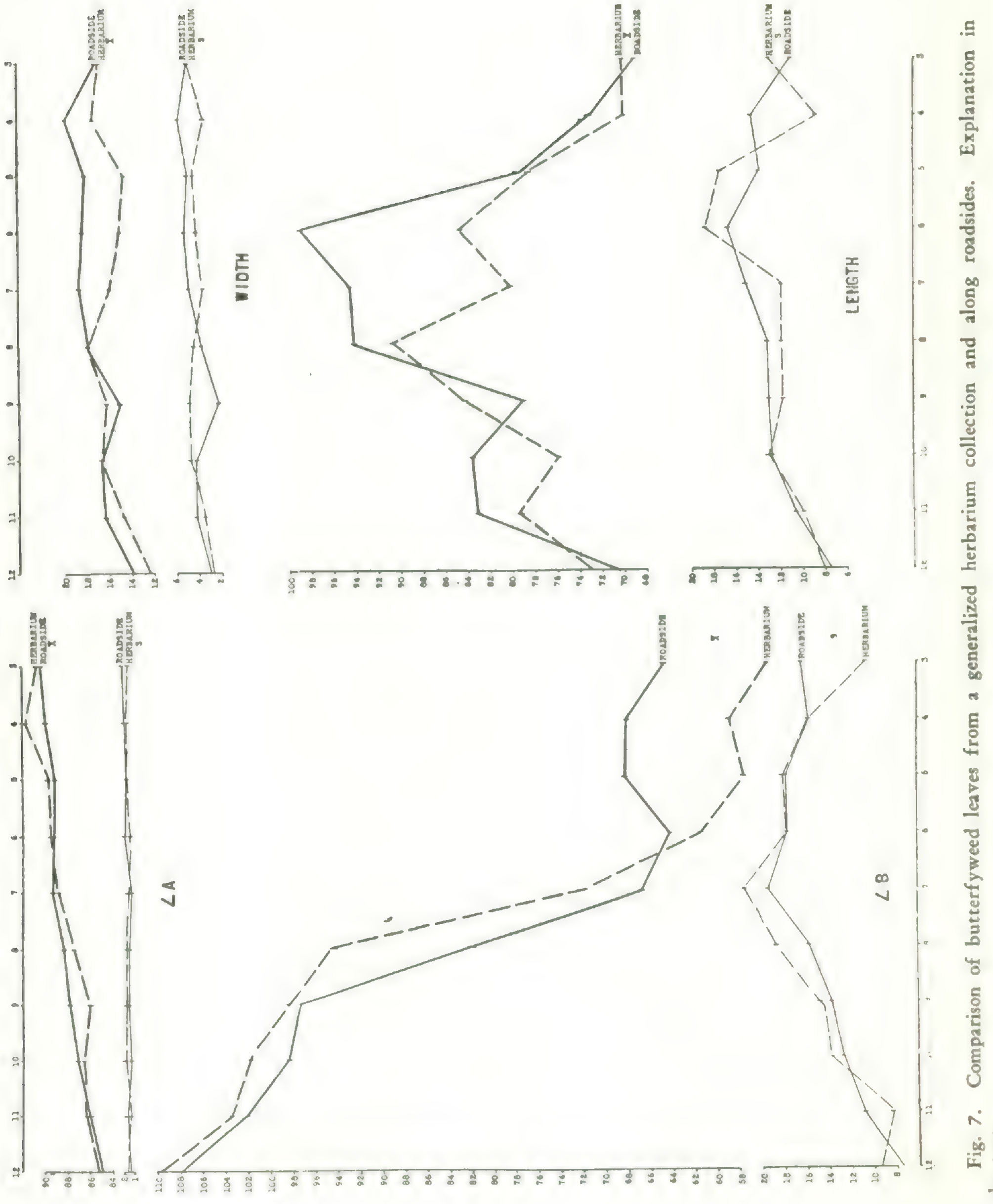


Fig. 7. Comparison of butterfyweed leaves from a generalized herbarium collection and along roadsides. Explanation in the text.

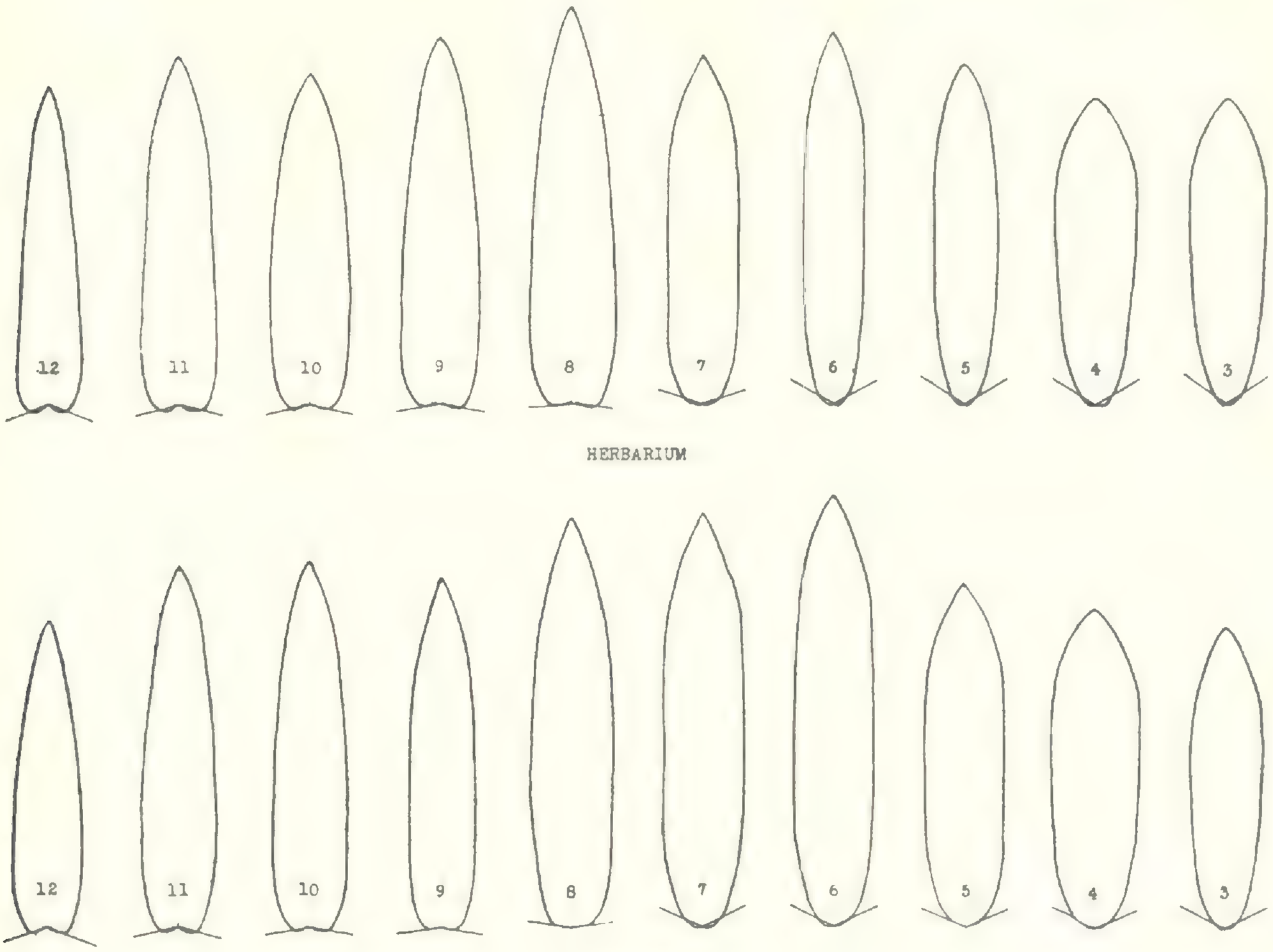


Fig. 8. Reconstruction of butterflyweed leaves from equivalent herbarium and roadside quadrats. Explanation in the text.

I conclude from our examination of the herbarium and roadside profiles that the details of the phenocontour maps obtained from herbarium specimens are reliable under the broad conditions of their compilation. More important, the observations of Wiegand (1935) and others, that hybridization is accelerated along roadsides and in disturbed areas, is affirmed and given quantitative expression.

Figure 8 reproduces models of leaves reconstructed according to the specifications of the ten herbarium and roadside quadrats, to illustrate our discussion pictorially as well as a commentary on our method of measurement. The basal lines by which ∠B is measured are included for the sake of easier comparison.

Figure 9 consists of a series of frequency histograms for ∠A and ∠B along the roadside profile, reassembled according to standard quadrats. The vertical curves connect the means of each histogram, and provide new representations of the clines we have been discussing. The distributions of the ∠A quadrats, considering the size of their samples, are nearly normal throughout. In the histograms for ∠B, however, a consistent positive skewing is noticeable in quadrats *7* to *3*. To the west, in quadrats *8* to *10*, a negative skewness is found, while the distributions of quadrats *11* to *12* are normal or essentially so. In the ∠B, therefore, the

♀ 12
∠ A
X̄=84.9
S= 1.4
N= 96
∠ B
X̄=108.0
S= 7.5
81
88
85
125
♀ 11
∠ A
X̄=86.0
S= 1.6
N= 58
∠ B
X̄=102.1
S= 10.8
82
90
75
130
♀ 10
∠ A
X̄=87.1
S= 1.3
N=104
∠ B
X̄= 98.4
S= 12.7
82
91
60
135
♀ 9
∠ A
X̄=87.8
S= 1.5
N= 13
∠ B
X̄= 97.3
S= 13.8
86
92
60
115
♀ 8
∠ A
X̄=88.8
S= 1.5
N= 95
∠ B
X̄= 81.9
S= 15.7
83
91
40
115
♀ 7
∠ A
X̄=89.3
S= 1.3
N= 87
∠ B
X̄= 66.7
S= 19.5
85
93
25
110
♀ 6
∠ A
X̄=89.2
S= 1.9
N= 32
∠ B
X̄= 64.1
S= 17.7
84
91
25
100
♀ 5
∠ A
X̄=89.1
S= 1.8
N=237
∠ B
X̄= 68.1
S= 17.8
84
95
25
110
♀ 4
∠ A
X̄=89.9
S= 2.0
N=120
∠ B
X̄= 68.1
S= 15.7
84
95
20
105
♀ 3
∠ A
X̄=90.4
S= 2.1
N=152
∠ B
X̄= 64.7
S= 16.3
84
96
30
105

Figure 9

quadrat distributions are skewed in the direction of introgression. The absence of consistent skewness in the ∠A histograms may be ascribed to the relatively less sensitivity of this measure; actually, however, I interpret it to be additional evidence of the quantitative nature of the ∠A genotype in contrast to the qualitative differences of the ∠B genotypes. This question will be considered in detail in a future series of studies on butterflyweed. Another aspect of the skewing of distributions in relation to the direction of gene flow will be presented shortly.

VI. Intra-subspecific Differentiation of *Asclepias tuberosa interior*

In the preceding discussions of the phenocontours of *Asclepias tuberosa,* we found that although minor microgeographic races may be observed in the eastern *A. t. tuberosa,* larger internal patterns, if they exist, are obscured by introgression with neighboring subspecies, the Floridian *A. t. Rolfsii* and the mid-western *A. t. interior.* The last named, however, has a range sufficiently large for us to extract for analysis the vast western portion of its distribution, which is not affected by introgressive gene flow with the eastern subspecies.

In this region, as we have learned from the phenocontours, it is possible to discern certain more or less definite trends in the median length, median width, apical taper (∠A), and nature of the base (∠B) of the leaves. These internal patterns may be rather vaguely distinguished by the method of quadrats through which the phenocontour maps were compiled, but they apparently are of such greater magnitude that they require a different method of analysis. The situation suggests an allegoric parallel with a picture printed by the half-tone process, in which the screened image must be viewed at a certain distance for best comprehension.

METHODS OF ANALYSIS

Methods for the analysis of the internal differentiation of *A. t. interior* are suggested by the phenocontour maps, in which the primary direction of modification usually is centrifugal from the Ozark plateau, the putative center of origin of the subspecies. This tendency is seen most clearly in the character of the leaf base, designated as ∠B; the leaves in the central Ozarks (*i. e.* quadrats *G11* and *G12*) being deeply cordate as a rule, but becoming successively less cordate in quadrats progressively outward in all directions from this center. At the periphery of the distribution, from southern Canada to northern Mexico, the leaves no longer are cordate, but more or less rounded or cuneate at the base, as in the eastern subspecies.

In Map VII, an arbitrary, solid line is drawn roughly from Toronto, Ontario, through San Antonio, Texas, and produced considerably to the southwest of the latter city; it is approximately midway between the central Ozarks and the crest of variability of the ∠B phenocontour map. To the right of this line, popu-

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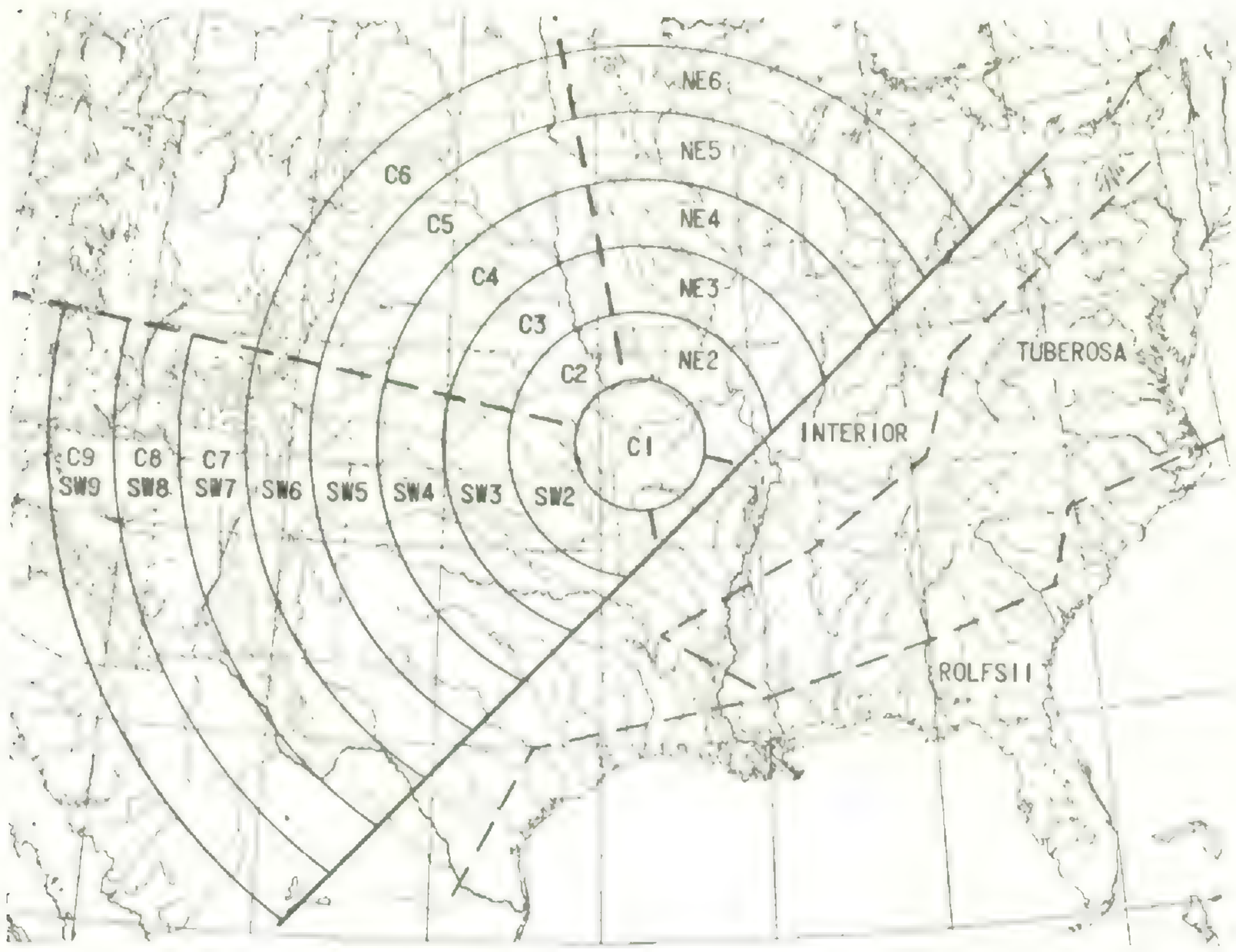
Fig. 9. ∠A and ∠B frequency histograms of butterflyweed leaves along a roadside profile, assembled into equivalent profiles. Explanation in the text.



Map VII. Method of study of intra-subspecific differentiation in *Asclepias tuberosa interior* by means of equidistant concentric circles.

lations of *A. t. interior* are increasingly affected by introgression with the eastern subspecies; to the left, evidence of introgression is absent or negligible. Any internal modification of ∠B which we will find in "true" ssp. *interior* surely must be taken into account in its effect on introgression with ssp. *tuberosa,* but we shall defer that aspect of the problem for the moment, confining our attention to strictly intra-subspecific differentiation to the left of our arbitrary boundary.

Since modification within *A. t. interior* is believed to be centrifugal from the central Ozarks, it is legitimate to test the hypothesis by projecting upon a map a series of equidistant concentric circles emanating from that point; this is accomplished in Map VII by using a center exactly midway between quadrats *GII* and *GI2*. Our procedure obviously must be made to agree as far as possible with the system of 120-mile quadrats previously employed in the phenocontour maps; consequently, the first circle, labelled *CI*, is inscribed with a radius of 120 miles about quadrats *GII* and *GI2*. The compass is then widened to increase the radius by 120 miles and a second circle is drawn outside *CI* and enclosing the circular area labelled as *C2*. In the map, this circle actually is drawn only to the left of the arbitrary solid line, but its course to the right must be visualized for the benefit of discussion which will follow. For our immediate purpose, *C2* is an arc rather than a circle. In the other circles, to *C6*, the same procedure is followed. Because *A. t. interior* extends farther to the southwest than to the northeast, the

outermost "circles" are lesser arcs touching the arbitrary solid line at only one point, but they, too, may be visualized as extending to the southeast of the introgression boundary, and thus are designated as *C7*, *C8*, and *C9*.

In reassigning statistics from the quadrats of the previous maps to the new circular populations, the arbitrary procedure is adopted of transfering to a given circle the data of only those quadrats whose exact center lies within its boundaries. Thus, in *C1*, although the periphery of the area intersects four other quadrats, only the centers of quadrats *G11* and *G12* satisfy our conditions, and the data of the other four are assigned, together with others similarly chosen, to *C2*. Similar assignment is practiced in the remaining circles.

An additional feature of Map VII which requires explanation are the two broken lines which intersect in the center of *C1*. These lines are drawn in order to separate from the concentric circles two equivalent series of concentric arcs lying in opposed directions, one to the northeast and labelled from *NE2* to *NE6*, the other to the southwest and labelled from *SW2* to *SW9;* the purpose of these will be explained shortly. Rather confusingly, I am afraid, the three southwestern-most arcs bear two sets of symbols, *C7* to *C9* and *SW7* to *SW9* for designation in different phases of our discussion, but the populations are the same.

THE EVIDENCE OF INTERNAL DIFFERENTIATION

∠B

Since our circle and arc populations will be provided by the quadrats of the phenocontour maps, two ways of using the quadrats in their new groupings suggest themselves, which we will illustrate with regard to the data for ∠B. In Table VI, the herbarium quadrats assigned to each circle have been broken down and the constituent cases thrown together in computing new circle means and the usual measures of variance. The centrifugal lowering of ∠B values which was intimated in an irregular fashion by the phenocontour map is seen to be a consistent tendency. In Table VII, on the other hand, the means of the means and the means of the standard deviations of the included quadrats of each circle are computed for comparison. Only slight deviations from the statistics of Table VI are found, and the centrifugal tendency is confirmed by either procedure.

It will be appreciated, however, that a curve drawn to the data of Table VII would be somewhat smoother than one drawn to the data of Table VI. I assume this to be due to unequal weighting caused by the numerous cases in well-collected quadrats and the fewer cases in quadrats less frequented by plant collectors. This inequality appears to be compensated in the calculation of the means of means and means of standard deviations, since a quadrat containing few cases is weighted equally to a quadrat containing many cases. In addition, of course, the method of Table VII is more convenient than that of Table VI; consequently I have used the former in subsequent computations.

The data of Table VII are presented graphically in fig. 10, in which the ordinate is in degrees of ∠B and the abscissa represents the equidistant circles

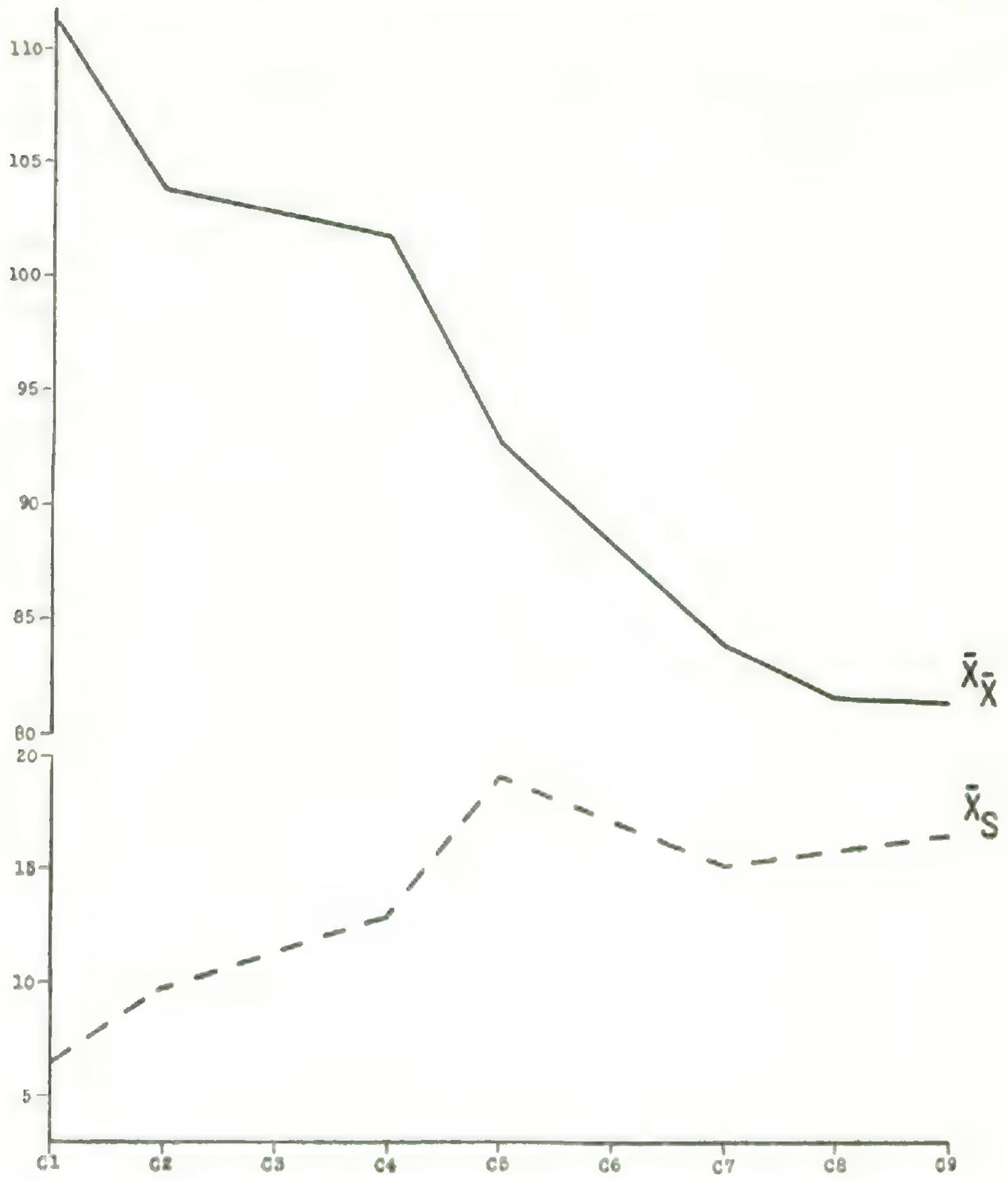


Fig. 10. ∠B means of means and means of standard deviations of *Asclepias tuberosa interior* in the central Ozarks and in equidistant concentric circles to the periphery of the subspecies range. Explanation in the text.

from the Ozark plateau. The means curve is seen to be remarkably even, with the exception of the interesting "hump" at circles *3* to *4*. The curve for the standard deviation means is still more interesting, since it rises from the lowest value, in circle *1* to a crest at circle *5;* then subsides to a somewhat lower plateau for the outermost circles.

The validity of the curves presented in fig. 10 may be tested by dividing the concentric circles into two equal, but opposed, series of concentric arcs to the southwest and to the northeast of the Ozark plateau. The primary purpose of these arcs is to withdraw for comparison two equivalent samples from the original populations; to further this end, the opposed arcs are isolated by the series of arcs to the northwest, upon which the labels of the circles appear. An additional advantage of our two series of arcs is that they traverse climatic regions which differ to a very marked degree: from the deserts of the southwestern United States and northern Mexico to the Ozarks, and from the Ozarks to the continental forests of

TABLE VI

∠B INDIVIDUAL CASES OF HERBARIUM QUADRATS REASSEMBLED INTO CONCENTRIC CIRCLES

(Means, standard errors, standard deviations, and coefficients of variation)

Arc	C1	C2	C3	C4	C5	C6	C7	C8	C9
N	31	213	223	176	225	85	44	32	64
$\bar{X}$	111.1 ± 1.2	104.2 ± 0.7	103.4 ± 0.8	100.1 ± 1.1	97.8 ± 1.2	84.5 ± 2.1	81.2 ± 2.5	83.6 ± 3.1	80.2 ± 2.1
s	6.4	10.0	12.0	14.8	18.0	18.9	16.5	17.4	16.6
V	5.8	9.6	11.6	14.8	18.4	22.4	20.3	20.8	20.7

TABLE VII

∠B MEANS OF HERBARIUM QUADRATS REASSEMBLED INTO CONCENTRIC CIRCLES

(Means of means and means of standard deviations)

Arc	C1	C2	C3	C4	C5	C6	C7	C8	C9
N	2	9	10	8	13	8	8	4	7
$\bar{X}\bar{x}$	111.2	103.8	102.7	101.8	92.8	88.4	83.9	81.6	81.4
$\bar{X}_s$	6.5	10.2	11.6	12.8	19.1	17.2	15.2	15.9	16.5

the Great Lakes. Thus we may expect to observe any influence of climate upon the phenotypic gradient.

Two final properties of the arc populations are worthy of attention. The northeastern arcs lie almost wholly in territory covered by the last glaciation, whereas the southwestern arcs apparently have been available for plant occupancy since the beginning of the Mesozoic or before. Furthermore, we have observed that colonies of butterflyweed are appreciably larger and more frequent in the northeastern arc, whereas in the southwestern arc the colonies are both smaller and more isolated. We may expect the three factors of climate, geological history, and relative population structure to have characteristic effects upon the internal differentiation of butterflyweed, as in other organisms. The method of analysis by two opposed arcs has so many advantages that it has been used not only with regard to ∠B, but to ∠A, median length, and median width as well. For the moment, however, we shall confine our attention to the first named.

Data for ∠B, analyzed by means of the two opposed arcs, are provided in Table VIII. In the uppermost panel of fig. 11, the data are presented graphically in a manner designed to simulate the geographic relationship of *CI* and the two sets of arcs, the ordinate scales in degrees being erected at the center, and the two sets of curves diverging to left (southwest) and right (northeast) respectively. The two sets of curves are strikingly similar, and both obviously confirm those previously obtained from the circle populations. Climate is seen to have nothing to do with expression of the phenotype.

The chief disagreement between the circle and the arc data is seen to be the accentuation of the "hump" of the means curves previously noted, occasioned by the relatively low values of arcs *2* and *3* in both the southwestern and the northeastern series. I assume this effect to be due to the failure of the diagonal, solid line noted in connection with Map VII entirely to exclude the influence of introgression with the eastern subspecies, and that the actual curves, if introgression were quite eliminated, would be appreciably smoother even than as depicted in fig. 10. I have not attempted to move the diagonal line farther to the left, however, because such action would result in reducing our populations sufficiently to impede our calculations. We are justified, however, in regarding the smooth means gradient of fig. 10 as being an understatement rather than an exaggeration.

It is important, finally, to emphasize the confirmation by the opposed arcs not only of the means of means presented in fig. 10, but also of the peculiar curve for the means of standard deviations, with its interesting crest of variability at circle *5*. It is important, also, to call attention to the similarity of this curve to the gradient of the standard deviations involved in the introgression of subspecies *interior* and *tuberosa* which were presented in fig. *7*.

The basic similarity of the gradients representing the introgression of subspecies *interior* and *tuberosa* (fig. *7*) and those involved in the internal differentiation of ∠B in *interior* strongly suggests that somewhat similar processes are in play. This is indicated most particularly by the confirmation of the crest of variability midway in the arc and circle gradients.

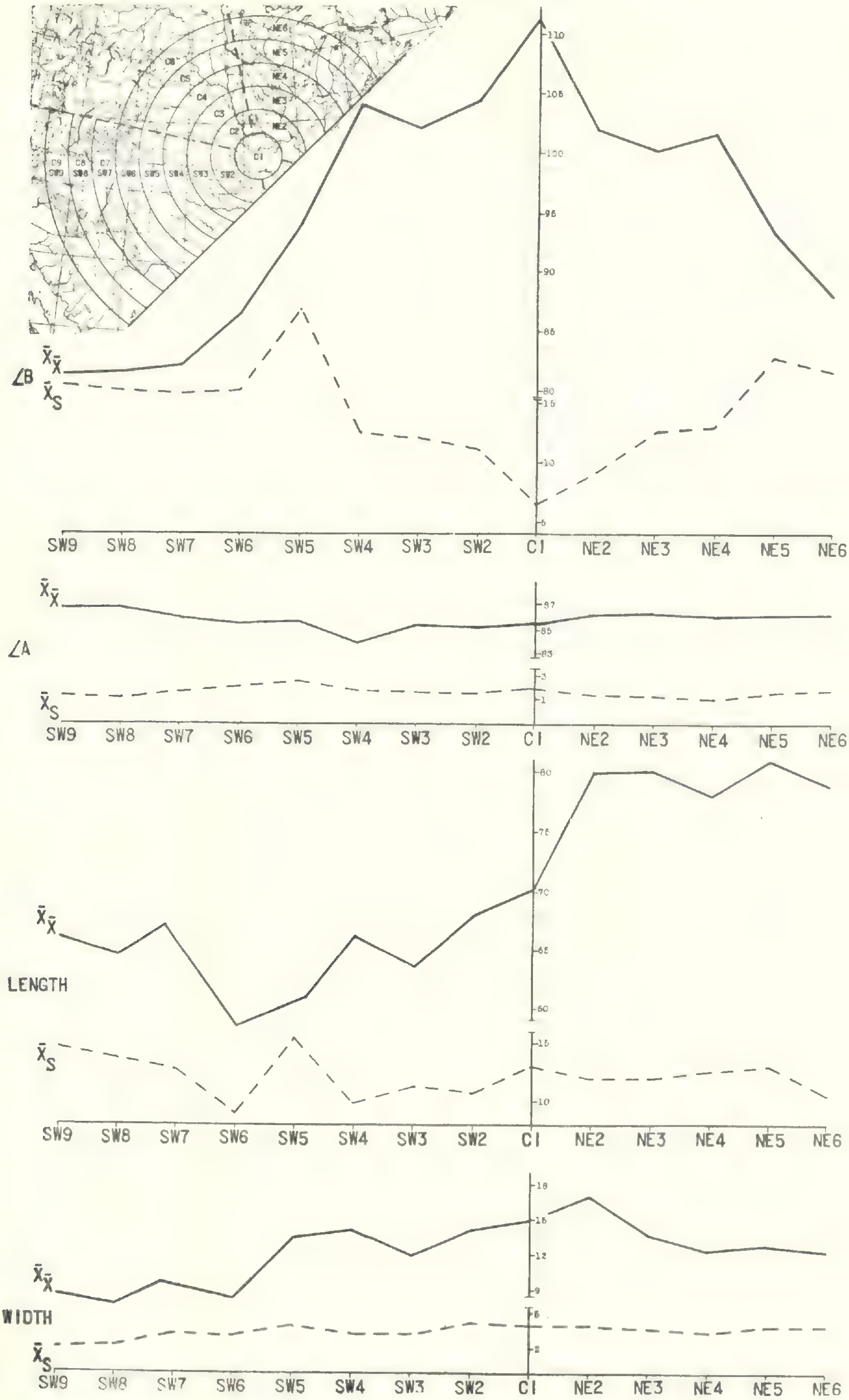


Fig. 11. Means of means and means of standard deviations of ∠B, ∠A, median length, and median width of *Asclepias tuberosa interior* in the central Ozarks and in equidistant series of arcs to the southwest and northeast. Explanation in the text.

TABLE VIII

∠B MEANS OF HERBARIUM QUADRATS REASSEMBLED INTO OPPOSED ARCS OF CONCENTRIC CIRCLES

(Means of means and means of standard deviations)

Arc	SW9	SW8	SW7	SW6	SW5	SW4	SW3	SW2	C1	NE2	NE3	NE4	NE5	NE6
N	7	4	6	2	4	3	4	4	2	3	3	4	7	4
$\bar{X}_{\bar{x}}$	81.4	81.6	82.1	85.4	94.1	104.0	102.1	104.4	111.2	101.9	100.2	101.6	93.4	87.9
$\bar{X}_s$	16.5	16.1	15.8	16.0	22.9	12.5	12.1	11.2	6.5	9.2	12.6	13.0	18.7	17.6

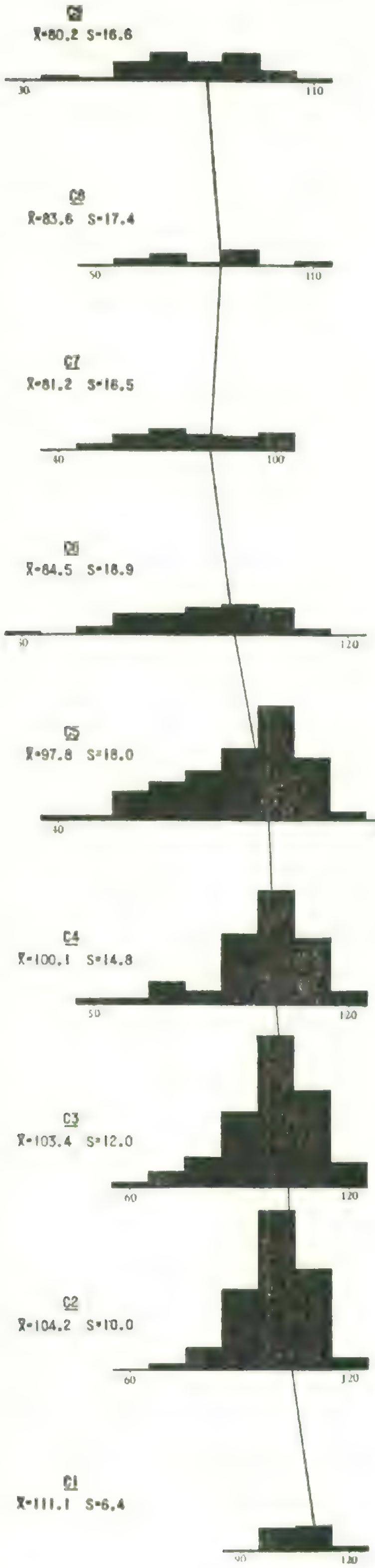
Since the gradients of the opposed arcs in glaciated and in unglaciated territory are essentially similar, I believe that we may visualize the leaves of *A. t. interior* in post-Pleistocene times, throughout its range, as being essentially like those with rounded to cuneate bases predominant to-day at the periphery of its distribution. In relatively recent times, probably only a few thousand years ago, a major genotypic change producing a deeply cordate leaf base would appear to have become established in the central Ozarks, and subsequently to have been diffused to outlying populations in the centrifugal manner which we have been discussing.

In the absence of detailed breeding and cytological evidence, we may only conjecture concerning the nature of this genic change. It is apparently multifactorial, as evidenced by the properties of its distributional frequencies (cf. fig. 12). One would expect a single mutation, even if having sufficient survival value, to be inoperative, and the simultaneous production of a sufficiently large number of concomitant mutations effecting the same character to be extremely unlikely. Since either translocation or inversion would be expected to reduce the frequency of crossing-over, it is difficult to see how the smooth gradient involved in the centrifugal modification of ∠B could be obtained through chromosomal rearrangement, as understood at present. I have in progress further genetical studies, which I hope will throw some light upon the nature of the supposed genotypic renovation of *A. t. interior*.

In this connection, however, it is worthy of note that I have found plants of the cordate-leaved populations of *A. t. interior* consistently to have more stems per plant, as well as more leaf nodes per stem, than in plants of the peripheral, narrow-based populations. It is natural to ascribe selective advantage to the former, because of their presumably greater reproductive potential, and we shall encounter confirmative statistical evidence of this inference presently.

Figure 12 consists of standard frequency histograms of ∠B in the nine circles extending from the central Ozarks to the periphery of the range of *A. t. interior* (exclusive of the zone of introgression with *A. t. tuberosa*). The vertical curve connects the means of the several histograms. Although surely distorted by the discrepant sample sizes, the symmetry of the distributions is remarkable in passing, centrifugally, from essential normality through increasing degrees of negative skewness to a less skewed, platykurtic form near the center of the gradient; the remaining figures become increasingly bimodal. An intimation of this trend was seen previously in the histograms of the roadside profile (fig. 9), in which the figure for *Q11* (partly within *C1*) is normal, whereas that for *Q12* (wholly within *C2*) is negatively skewed.

In connection with fig. 9, we remarked that skewing of the distributions is rather consistently in the direction of the introgressing subspecies parameters, and thus that it points toward the direction of gene flow. A more likely explanation of the skewing, however, is provided in fig. 12, which happens to be *away* from the direction of gene flow. In other words, skewing in these figures does not indicate the direction of gene flow, but probably merely the distribution of domi-



nance, as suggested by Fisher, Immer, and Tedin (1932). Consequently, in the gradual development of bimodality toward the periphery of the range, we might infer the gradual loss of dominance in both types. I assume that if our range were sufficiently great, we might thereafter witness the emergence of increasing dominance of the ancestral genotype.

Although it may be rather rash to continue speculation, I am inclined toward the opinion that in the centrifugal differentiation of ∠B within *A. t. interior*, as in the introgression of that subspecies with *A. t. tuberosa*, genic amalgamation is effected by migration, cross-fertilization, and redistribution of the genotypes through crossing-over. I would assume the bimodality of our peripheral populations to indicate relatively early steps in this process. The eventual emergence of the Ozark strain as dominant I would predict by virtue of its supposed selective advantages.

At this point I would wish to insert an analysis of a roadside profile from the central Ozarks through the circles, similar to that by which the introgression of subspecies *interior* and *tuberosa* was studied. Since circumstances have prevented me from gathering the necessary data, Table IX is substituted, in which will be found statistics of a random assortment of natural butterflyweed colonies collected in the central Ozarks and in the southwestern and northeastern arcs. As incomplete as the evidence may be, we may observe additional confirmation of the centrifugal effect; we may see that here, also, as in the introgressing subspecies, redistribution of the genotypes is not an orderly diffusion, but proceeds from colony to colony with different

Fig. 12. Distribution of ∠B in 9 equidistant circles from the central Ozarks to the periphery of the range of *A. t. interior*. Explanation in the text.

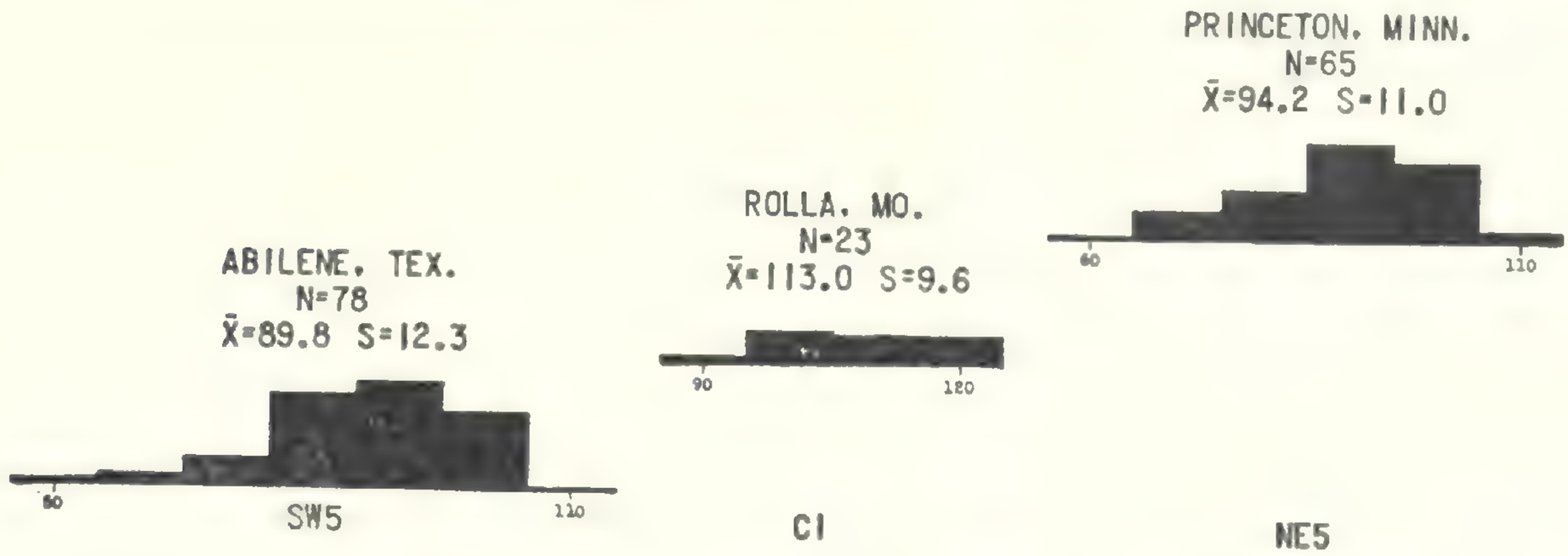


Fig. 13. Distribution of ∠B in 3 colonies of *A. t. interior*. Explanation in the text.

velocity rates, depending on the genic constitution of the reproducing zygotes.

Figure 13 consists of frequency histograms of three natural colonies of *A. t. interior:* one drawn from the central Ozarks, the other two from arcs *SW5* and *NE5*, from left to right, respectively. The figures confirm the properties of the artificial populations which were discussed with reference to fig. 12. Bimodal distributions from the far southwest are not available because of the small population sizes in that region.

If we return, in closing, to the complementary curves for ∠B in the southwest and northeast arcs, reproduced in the uppermost panel of fig. 11, we may remember that the first evidence of the genetic basis of the centrifugal effect was received in view of the very great climatic difference of the territories included. Whether toward the Sonoran deserts or the Canadian forests, the phenotypic gradients apparently are not directly affected. That is to say that the concentric lowering of ∠B values, *per se*, is not environmental.

In the relative rates of transmission of the new gene arrangement, however, there is evidence that climate plays a positive role. For in the more equable climates of the northeastern arcs, the gradient for the means of means is more smooth than is that in the hotter, more arid southwestern arcs, and the means of the corresponding arcs are consistently somewhat lower. The curve for the means of standard deviations is more even in the northeastern arcs as well, and the crest of variability is somewhat lower. Genic diffusion obviously is more rapid in the northeastern arcs because the favorable climate allows the incidence of both larger and more frequent colonies of the plant.

In the remaining paragraphs of this section, the data for ∠A, median length, and median width are treated similarly by the comparison of the southwestern and northeastern arc populations. Data are provided in Tables X, XI, and XII, respectively, and presented graphically in fig. 11. In all three characters evidence of genetic drift, with or without the directing influence of natural selection, appears to be the chief phenomenon of interest.

Before continuing, it may be well to emphasize again what I take to be the most important properties of the two series of arcs in this connection, *viz.*, the rather uniformly equable climate of the northeastern arcs, with their relatively

TABLE IX

MEASUREMENTS OF LEAVES OF *ASCLEPIAS TUBEROSA INTERIOR* ASSEMBLED ACCORDING TO NATURAL COLONIES FROM NORTHEAST TO SOUTHWEST OF THE SUBSPECIES RANGE

(Means, standard errors, standard deviations, and coefficients of variation; angles in degrees, length and width in millimeters)

Arc	Colonies		∠A			∠B			Length			Width		
	Location	N	$\bar{X}$	s	V	$\bar{X}$	s	V	$\bar{X}$	s	V	$\bar{X}$	s	V
NE5	Long Siding, Mille Lacs Co., Minn.	8	86.9 ± 0.5	1.3	1.5	82.6 ± 4.7	12.4	15.0	82.9 ± 5.0	13.1	15.8	12.5 ± 1.4	3.6	28.8
"	Princeton #1, Sherburne Co., Minn.	65	86.1 ± 0.2	1.4	1.6	94.2 ± 1.4	11.0	11.7	83.8 ± 1.4	11.3	13.5	12.9 ± 0.4	3.1	24.0
"	Princeton #2, Sherburne Co., Minn.	29	87.9 ± 0.1	0.6	0.7	90.9 ± 2.0	10.8	11.9	79.4 ± 2.0	10.4	13.1	9.8 ± 0.3	1.7	17.3
"	Elk River #1, Sherburne Co., Minn.	31	87.2 ± 0.2	1.3	1.5	91.5 ± 1.8	10.1	11.0	82.5 ± 2.1	11.4	13.8	12.0 ± 0.4	2.2	18.3
"	Elk River #2, Sherburne Co., Minn.	22	85.9 ± 0.4	1.8	2.1	88.6 ± 3.2	14.7	16.6	83.5 ± 2.4	11.0	13.2	13.3 ± 1.1	5.1	38.3
"	Elk River #3, Sherburne Co., Minn.	23	86.5 ± 0.2	0.9	1.0	89.6 ± 2.9	13.5	15.1	86.3 ± 2.4	11.4	13.2	11.3 ± 0.4	1.7	15.0
"	Snail Lake #1, Ramsey Co., Minn.	31	87.2 ± 0.2	1.2	1.4	85.4 ± 3.0	17.4	20.4	77.7 ± 2.8	15.6	20.1	10.2 ± 0.6	3.0	29.4
"	Snail Lake #2, Ramsey Co., Minn.	28	86.2 ± 0.2	1.2	1.4	85.4 ± 2.3	12.1	14.2	80.8 ± 1.8	9.4	11.6	11.5 ± 0.5	2.5	21.7
"	Snail Lake #3, Ramsey Co., Minn.	55	87.8 ± 0.2	1.2	1.4	86.7 ± 2.1	15.3	17.6	84.2 ± 1.6	11.7	13.9	10.5 ± 0.3	2.4	22.8
"	Cannon Falls #1, Dakota Co., Minn.	17	85.6 ± 0.3	1.3	1.5	95.2 ± 1.8	7.3	7.7	86.5 ± 2.8	11.0	12.7	12.9 ± 0.6	2.4	18.6
"	Cannon Falls #2, Dakota Co., Minn.	7	87.6 ± 0.3	0.7	0.8	101.4 ± 3.4	9.1	9.0	85.0 ± 3.6	9.4	11.1	10.4 ± 1.0	2.7	25.9
"	Hampton, Dakota Co., Minn.	4	87.8 ± 0.4	0.9	1.0	79.1 ± 2.6	5.2	6.6	86.0 ± 2.6	11.2	13.0	11.0 ± 1.1	2.2	20.0
"	River Falls, Pierce Co., Wis.	11	85.6 ± 0.3	0.9	1.2	91.4 ± 2.7	8.4	9.2	89.5 ± 3.0	9.5	10.6	15.1 ± 0.3	1.0	6.6
"	Hertel, Burnet Co., Wis.	11	84.8 ± 0.6	1.8	2.1	91.5 ± 2.3	7.5	8.2	83.7 ± 2.7	8.4	10.0	11.8 ± 0.5	1.7	14.3
"	Kalamazoo, Schoolcraft Co., Mich.	13	86.5 ± 0.3	1.0	1.2	107.1 ± 1.7	6.1	5.7	93.5 ± 3.1	11.0	11.8	19.5 ± 0.8	2.8	14.4
NE4	Silver Lake, Palo Alto Co., Iowa	20	85.5 ± 0.2	0.8	0.7	112.8 ± 1.5	6.8	6.0	86.4 ± 1.6	7.0	8.1	13.0 ± 0.3	1.1	8.5

TABLE IX *(Continued)*

Arc	Colonies		∠A			∠B			Length			Width		
	Location	N	$\bar{X}$	s	V	$\bar{X}$	s	V	$\bar{X}$	s	V	$\bar{X}$	s	V
NE4	Ruthven, Clay Co., Iowa	8	85.9 ± 0.2	0.4	0.5	110.9 ± 1.9	4.9	4.4	71.2 ± 2.8	7.2	10.1	10.0 ± 0.8	2.1	21.0
NE3	Wilton Junction, Muscatine Co., Iowa	12	86.5 ± 0.3	0.9	1.0	103.8 ± 3.0	9.8	9.4	99.2 ± 3.9	13.0	13.1	17.5 ± 1.2	3.8	21.1
”	Pocahontas, Pocahontas Co., Iowa	23	86.0 ± 0.4	1.9	2.2	103.9 ± 2.8	12.6	12.1	68.9 ± 2.1	10.0	14.5	10.0 ± 0.5	2.5	25.0
NE2	Murray, Clarke Co., Iowa	25	86.3 ± 0.3	1.5	1.7	103.5 ± 0.5	2.8	2.7	74.1 ± 2.3	11.1	15.0	10.5 ± 0.6	3.1	29.5
”	La Plata, Macon Co., Mo.	19	86.4 ± 0.4	1.5	1.7	98.3 ± 2.3	9.6	9.8	80.4 ± 2.3	11.2	13.9	14.0 ± 0.9	3.7	26.4
C1	Stanton, Franklin Co., Mo.	20	84.6 ± 0.6	2.6	3.1	99.3 ± 2.8	12.4	12.5	87.6 ± 3.4	15.0	17.2	18.8 ± 1.1	4.9	27.1
”	Rolla, Phelps Co., Mo.	23	86.5 ± 0.2	1.2	1.4	113.0 ± 2.0	9.6	8.5	76.7 ± 2.8	13.1	17.1	16.8 ± 0.9	4.4	20.2
SW3	Claremore, Rogers Co., Okla.	8	84.4 ± 0.4	1.0	1.2	115.1 ± 1.2	3.2	2.8	72.0 ± 5.7	14.8	20.6	12.1 ± 1.5	3.8	31.4
”	Hugo, Choctaw Co., Okla.	28	86.1 ± 0.3	1.4	1.6	111.2 ± 1.5	7.8	7.0	79.8 ± 2.1	11.0	13.8	13.7 ± 0.7	3.6	26.3
”	Colgate, Coal Co., Okla.	7	84.7 ± 0.3	0.8	0.9	99.5 ± 2.2	5.5	5.5	46.0 ± 3.2	7.9	17.2	9.9 ± 0.8	1.9	19.2
SW5	Hays, Ellis Co., Kans.	14	83.9 ± 0.4	1.5	1.8	111.7 ± 1.7	6.1	5.5	73.2 ± 2.9	10.4	14.2	17.2 ± 1.1	3.9	22.7
SW6	Abilene, Callahan Co., Tex.	78	84.7 ± 0.2	2.0	2.4	89.8 ± 1.4	12.3	13.7	55.9 ± 0.4	3.7	6.6	10.9 ± 1.1	9.6	17.2
SW7	Guadalupe Mts., Eddy Co., N. M.	6	85.8 ± 0.5	0.8	0.9	90.3 ± 2.9	5.0	5.5	92.3 ± 4.2	7.2	7.8	11.5 ± 0.6	1.0	8.7
SW8	McKittrick Canyon, Culberson Co., Tex.	6	86.9 ± 0.4	0.8	0.9	90.7 ± 5.7	12.8	14.1	79.7 ± 7.9	17.6	22.1	10.9 ± 1.1	2.6	23.8
	Pinos Altos Mts., Grant Co., N. M.	3	86.0 ± 0.6	0.9	1.0	72.0 ± 6.9	9.7	13.5	55.3 ± 4.5	6.4	11.6	7.0 ± 0.7	1.0	14.3

TABLE X

∠A MEANS OF HERBARIUM QUADRATS REASSEMBLED INTO OPPOSED ARCS OF CONCENTRIC CIRCLES

(Means of means and means of standard deviations)

Arc	SW9	SW8	SW7	SW6	SW5	SW4	SW3	SW2	C1	NE2	NE3	NE4	NE5	NE6
N	7	4	6	2	4	5	4	4	2	3	3	4	7	4
$\bar{X}_{\bar{x}}$	87.7	86.7	85.9	86.4	85.6	83.8	85.4	85.2	85.5	86.2	86.4	86.1	86.2	86.3
$\bar{X}_{s}$	1.3	1.1	1.6	2.1	2.6	1.8	1.7	1.6	2.0	1.5	1.4	1.1	1.7	1.9

TABLE XI

MEDIAN LENGTH MEANS OF HERBARIUM QUADRATS REASSEMBLED INTO OPPOSED ARCS OF CONCENTRIC CIRCLES

(Means of means and means of standard deviations)

Arc	SW9	SW8	SW7	SW6	SW5	SW4	SW3	SW2	C1	NE2	NE3	NE4	NE5	NE6
N	7	4	6	2	4	5	4	4	2	3	5	4	7	4
$\bar{X}_{\bar{x}}$	66.0	64.5	67.0	58.3	60.8	66.1	63.5	67.9	70.1	80.0	80.1	78.0	80.9	78.8
$\bar{X}_{s}$	14.6	13.7	12.7	8.9	15.4	9.8	11.3	10.7	13.0	12.0	12.0	12.6	13.0	10.5

TABLE XII

MEDIAN WIDTH MEANS OF HERBARIUM QUADRATS REASSEMBLED INTO OPPOSED ARCS OF CONCENTRIC CIRCLES

(Means of means and means of standard deviations)

Arc		SW9	SW8	SW7	SW6	SW5	SW4	SW3	SW2	C1	NE2	NE3	NE4	NE5	NE6
	N	7	4	6	2	4	5	4	4	2	3	5	4	7	4
	$\bar{X}_r$	8.5	7.7	9.6	8.3	13.5	14.1	12.0	14.1	15.0	17.0	13.7	12.4	12.8	12.4
	$\bar{X}_s$	2.0	2.2	3.2	3.1	3.9	3.3	3.3	4.2	4.0	4.0	3.8	3.4	3.9	4.0

larger and more frequent colonies of butterfly-weed; and the increasingly hot, arid climate of the southwestern arcs, in which the colonies are observed to become smaller and less frequent. Of less obvious bearing to our discussion is the probability that the southwestern populations are of greater antiquity than are those of the northeast.

∠A

In view of the relatively narrow interval range of this measure, the monotonous regularity of the curve for ∠A (fig. 11, middle panel) may be somewhat deceptive. Even so, it is apparent that in arc *SW4* (western Great Plains) there is a definite tendency for more abruptly tapered leaves, while in the far southwest the leaves predominantly are more gradually tapered than the normal. We have observed these tendencies previously in the phenocontour maps. Since both extremes occur in hot, arid or semi-arid land, where colonies are relatively small and infrequent, and apparently are not parts of a definite geocline, I conclude that we are observing a rather poor example of genetic drift, in which the influence of natural selection is absent or negligible.

LENGTH AND WIDTH

In the curves for median length and median width (fig. 11, two lower panels), the interaction of genetic drift and selective pressure toward the establishment of microphyllous types, so characteristic of xerophytic vegetation, appears in the southwestern arcs with almost schematic clarity. In general, length is correlated with width; but in the northeastern arcs we see that the two characters may behave independently, the length regularly being considerably greater than in the Ozarks, while the width is generally somewhat less. The various curves presented in fig. 11 appear to testify to the individuality of the genetic mechanisms responsible for all four phenotypes,

and their freedom of action under the pressures of both natural selection and the breeding structure of the populations.

RELATION OF THE CENTRIFUGAL EFFECT IN ∠B TO INTROGRESSION

Having demonstrated the existence of centrifugal modification of the leaf base in genetically more or less "pure" *Asclepias tuberosa interior*, an attempt should be made to apply what we have just learned to the problem of introgression of that subspecies with *A. t. tuberosa*.

In the lower panel of fig. 14, appears a map of the east-central United States from the Ozark plateau to the Atlantic coast. Three features of our previous discussions are superimposed upon this map: the concentric circles of Map VII as they would appear if projected to the east of the boundary of introgression, the horizontal rank of quadrats from *G3* to *G11* of the phenocontour maps (which is chosen because it coincides with the diameter of the concentric circles), and the position of the crests of variability between subspecies *interior*, *tuberosa*, and *Rolfsii* as determined in Map IV. Since the width of the circular areas corresponds to the sides of the quadrats, it is possible to effect a fairly satisfactory comparison of the two sets of data.

In the upper panel of fig. 14, the ordinate is in degrees of ∠B and the abscissa records the positions of the coinciding circles and quadrats as they appear in the map immediately below. The uppermost curve, borrowed from fig. 10, represents the centrifugal modification of ∠B which we might expect to obtain in this region if there were no introgression with the eastern *A. t. tuberosa*. The lower continuous curve represents the actual gradient of the quadrat means, taken from Table III, indicative of the effect of introgression of *A. t. interior* with the eastern subspecies.

If we refer back a moment to the ∠B curves in fig. 7, which were obtained along the horizontal rank of quadrats from *F3* to *F12*, their basic similarity to the quadrats curve in fig. 14 is apparent; in all three curves the influence of the "hump" noted in the circles and arcs gradients may be observed. We shall attempt to provide possible explanations of this feature in paragraphs which will follow, but for the moment it is sufficient to note the participation of the centrifugal effect in introgression of the two subspecies.

Before continuing farther, it is necessary to call attention once again to evidence of the introgression of *A. t. tuberosa* with the Floridian *A. t. Rolfsii*, namely, the abrupt rise of ∠B values at the eastern end of the quadrats curve in fig. 14. It may readily be appreciated that the more or less hastate or cordate leaf base characteristic of the latter subspecies would produce a relatively high ∠B value; and its proximity to the crest of variability between the two subspecies leaves little doubt concerning the change of gradient of which we speak. The Floridian subspecies, in fact, most probably also is concerned in the similar gradient changes

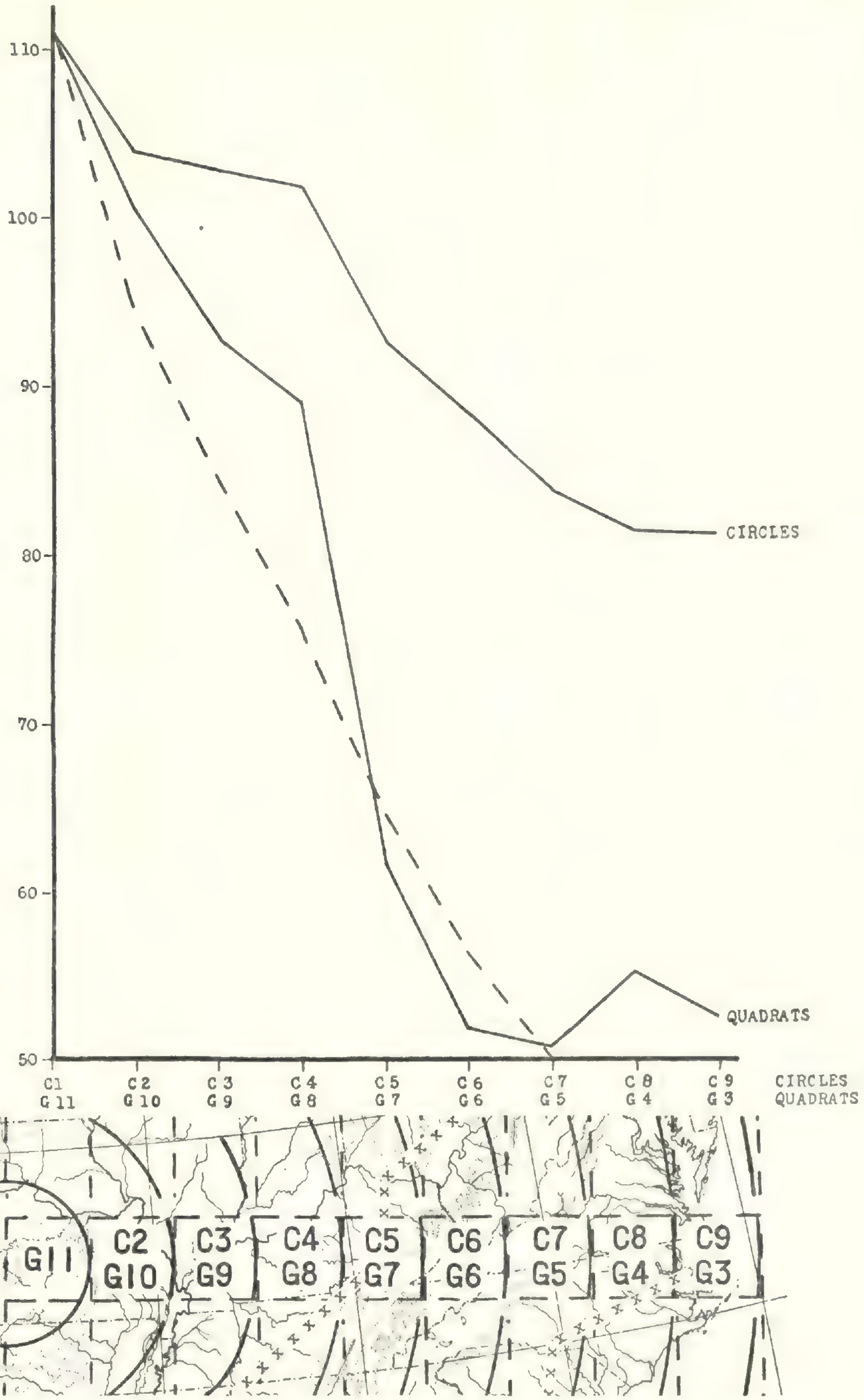


Fig. 14. Comparison of ∠B quadrat means as expected with simple gene diffusion and as actually obtained in the introgression of *A. t. interior* and *A. t. tuberosa.* Explanation in text.

seen at the eastern end of the ∠B curves in fig. 7. Since our biometric measures have been designed for use only with the other subspecies, the recurrent influence of *Rolfsii* is rather annoying, however instructive.

Hemmed in by *A. t. interior* on the west and northwest, and by *A. t. Rolfsii* on the south and southeast, little remains of *A. t. tuberosa* which may be called genetically pure. Under such conditions, it is impossible to distinguish internal population patterns except upon the lowest level, and very hazardous to speculate concerning the original subspecies parameters. In the absence of any evidence to the contrary, I assume that there is no concentric modification of the leaf base in *A. t. tuberosa* such as we have just demonstrated in *A. t. interior*. Since the quadrat populations upon the Atlantic coast farthest from the probable influence of introgression vary roughly between 47° and 55° with respect to ∠B, I am estimating a leaf base of 50° as a convenient approximation of the characteristic of "pure" *A. t. tuberosa*.

An interesting aspect of the quadrats, or introgression, gradient between subspecies *interior* and *tuberosa* is shown by use of the broken line in fig. 14. This line, purely a hypothesis, is drawn from quadrat *G11* in the central Ozarks to quadrat *G5* in the eastern Appalachians, where the herbarium sample approximates the estimated ∠B parameter of "pure" ssp. *tuberosa*.

The hypothesis of the broken line is that there is a perfectly balanced diffusion of genes between subspecies *interior*, emanating from *G11*, and *tuberosa*, emanating from *G5*, in much the same manner as we might visualize the diffusion of the molecules of two equally miscible inorganic compounds. Since we have good evidence of the centrifugal lowering of ∠B values in *interior*, and are assuming the stability of a value of 50° in *tuberosa*, the broken line is plotted at equally graded intervals between the "circles" curve and the 50° abscissa, to show 100 per cent *interior* and 0 per cent *tuberosa* influence at quadrat *G11*, 0 per cent *interior* and 100 per cent *tuberosa* influence at *G5*, 50 per cent influence of both *interior* and *tuberosa* at *G8*, and so forth, for the intervening quadrats. The points along the broken line, rounded for convenience, as well as the percentage values of the corresponding points along the quadrats curve, are provided in Table XIII.

A comparison of the broken line with the quadrats curve in fig. 14 will show the consistent way in which they differ, for we see that the *interior* influence is greater toward the western half of the cline, and that of *tuberosa* greater toward the eastern half than we would expect if genes were exchanged equally between the two subspecies, other factors being removed. The surplus *interior* influence is seen to increase toward the east, progressively from *G11* to *G8*, whereas that of *tuberosa* would appear to decrease toward the west. Finally, in *G5*, possibly because we have set the estimated parameter of "pure" *tuberosa* too low, the value obtained from the quadrat data appears to show the influence of *Rolfsii*. The latter feature may be neglected as inconsequential for our immediate purpose; but the centrifugal increase of *interior* influence and decrease of *tuberosa* influence is of more interest.

TABLE XIII

COMPARISON OF ∠B QUADRAT PERCENTAGES AND MEANS AS EXPECTED WITH SIMPLE GENE DIFFUSION AND AS ACTUALLY OBTAINED IN THE INTROGRESSION OF *A. T. INTERIOR* AND *A. T. TUBEROSA*

(Explanation in the text)

Quadrat	G11	G10	G9	G8	G7	G6	G5
% *int./tub.* expected	100/0	83/17	67/33	50/50	33/67	17/83	0/100
% *int./tub.* obtained	100/0	94/6	81/19	76/24	27/73	5/95	2/98
$\bar{X}$ expected	111.2	94.6	85.3	75.9	63.7	56.5	50.0
$\bar{X}$ obtained	111.1	100.5	92.9	89.1	61.7	52.0	50.8
d/σ	0.0	3.5	2.1	2.2	0.3	0.8	0.2

Table XIII also presents the quadrat means expected with simple gene flow of the sort we hypothesize, together with the means actually obtained. Finally, the coefficient of abmodality, d/σ, is calculated. A frequent biometric practice is to regard d/σ values >2 as significant and values <2 as probably not significant. If we apply this arbitrary rule to our calculations, we find that the centrifugal increase of *interior* influence probably is significant, while that of *tuberosa* probably is not. The means obtained from the quadrat samples in *G7*, *G6*, and *G5*, therefore, may be regarded as coinciding sufficiently with the hypothesis, and the apparently surplus *tuberosa* influence as dubious.

Several explanations present themselves to account for the interesting properties of the introgression gradient; they are not mutually exclusive nor do they exhaust all possibilities:

1. Natural Selection.—In the previous discussion of the centrifugal effect proper, we have seen that the larger number of flowering stems per plant, as well as the increased general vigor, characteristic of the cordate-leaved race of subspecies *interior*, almost certainly would tend to increase the reproductive potential of the plants, and thus might well be of importance in natural selection. Hence, the selective superiority of *interior* might enable it to extend more rapidly and perhaps into a greater variety of habitats than subspecies *tuberosa*. If this explanation is worthy of consideration in connection with the aggressive role of *interior* in introgression with *tuberosa*, it probably is worthy of consideration as a causative agent in the change of gradient ("hump") which we noted originally in fig. 11; *i. e.*, the supersedure of the ancestral race of *interior* with cuneate- or round-based leaves by the younger, cordate-leaved race from the central Ozarks may be due to selective superiority associated with the latter.

2. *Migration Pressure.*—The quadrats gradient of fig. 14 recalls the obvious fact that plants tend to migrate outward from their centers of dispersal through the agency of dissemination and other methods of transport. In this instance, the migratory powers of *interior* may be taken as greater than those of *tuberosa.* Since the seeds of *Asclepias* are classical examples of wind-dissemination, we may construe the direction of the prevailing winds in this section of the United States, from west to east, as favoring this argument.

3. *Dominance.*—The gradient may be indicative of the relative dominance of the *interior* genotype and the recessiveness of that of *tuberosa.* According to Fisher's theory of dominance, I take it that this possible "explanation" is merely a corollary of the first.

4. *Genetic Structure.*—The different degrees of aggressiveness of *interior* and *tuberosa,* on the other hand, may be due to a difference in the structural natures of the respective genotypes which makes the diffusion of the "*interior* influence" somewhat more rapid than that of *tuberosa.* For example, a large gene complex, rather diffuse with respect to loci, might be more easily redistributed in crossing-over than a smaller, more compact one. This suggestion is wholly conjectural and cannot be supported by our present technique, although it deserves theoretic consideration.

If the surplus influence of *interior* which we have just demonstrated with regard to ∠B is due to migration pressure, we would expect to find a similar surplus with regard to ∠A. Accordingly, fig. 15 compares the ∠A quadrat means as expected in simple diffusion of genes and as actually obtained in the introgression of *A. t. interior* and *A. t. tuberosa.* The method is precisely the same as that employed in the construction of fig. 14, the estimated parameter of "pure" *interior*

TABLE XIV

COMPARISON OF ∠A QUADRAT PERCENTAGES AND MEANS AS EXPECTED IN SIMPLE GENE DIFFUSION AND AS ACTUALLY OBTAINED IN THE INTROGRESSION OF *A. T. INTERIOR* AND *A. T. TUBEROSA*

(Explanation in the text)

Quadrat	G11	G10	G9	G8	G7	G6	G5
% *int./tub.* expected	100/0	83/17	67/33	50/50	33/67	17/83	0/100
% *int./tub.* obtained	96/4	93/7	60/40	46/54	30/70	16/84	4/96
$\bar{X}$ expected	85.5	86.5	87.4	88.2	89.2	90.0	91.0
$\bar{X}$ obtained	85.7	85.9	87.7	88.5	89.4	90.1	91.1
d/σ	0.3	1.3	0.6	0.6	0.2	0.1	0.5

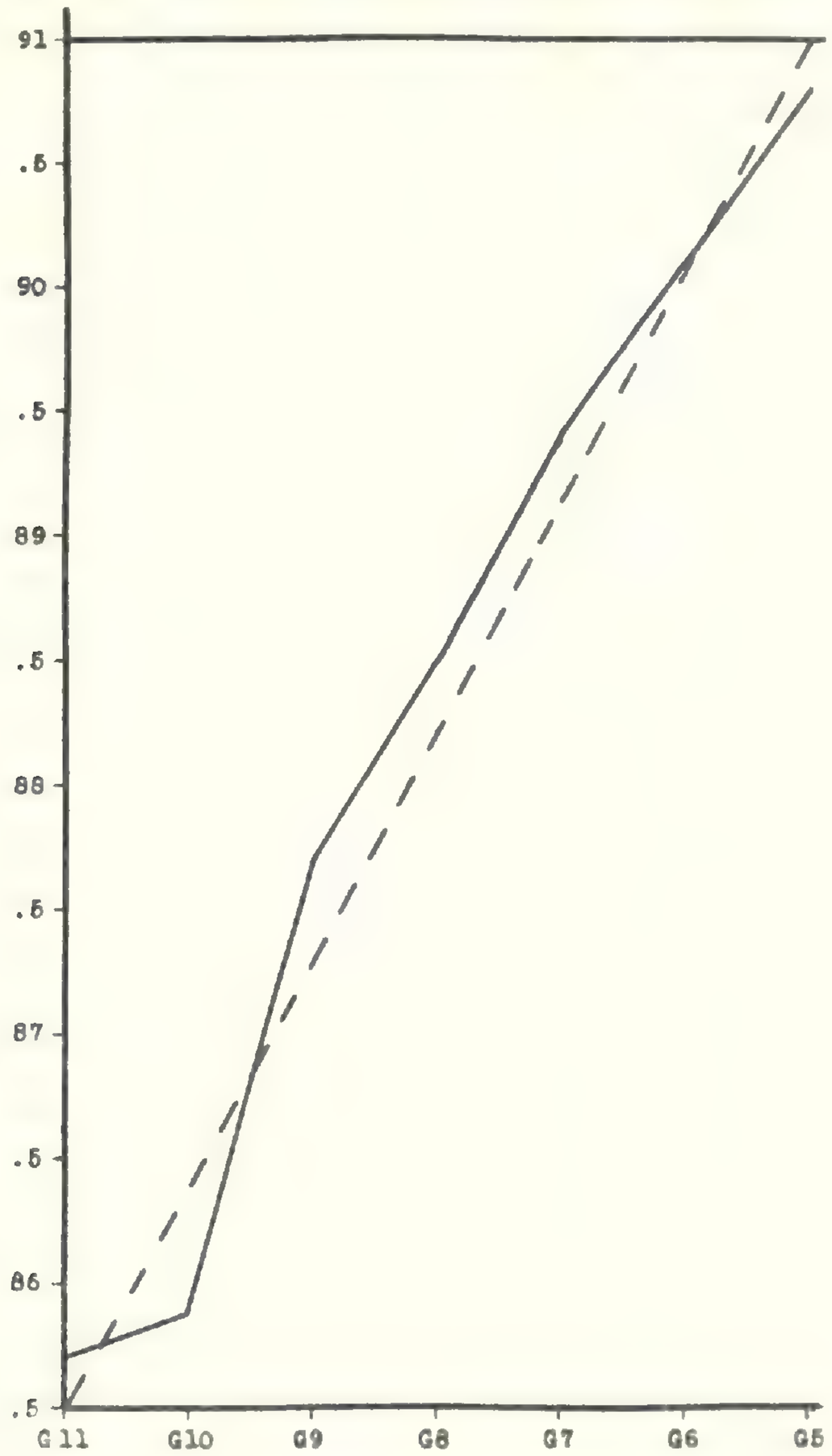


Fig. 15. Comparison of ∠A quadrat means as expected with simple gene diffusion and as actually obtained in the introgression of *A. t. interior* and *A. t. tuberosa*. Explanation in text.

in this case being 85.5° and that of "pure" *tuberosa* 91°. The percentages of "influence" and means, expected and obtained, as well as d/σ values for each quadrat, are provided in Table XIV.

In spite of the fact that the ordinate scale of fig. 15 is made ten times greater than that of fig. 14, to compensate for the correspondingly discrepant range scales of ∠B and ∠A, the close correspondence of the broken line representing the hypothesis and the continuous curve of the actual genocline is apparent. The small d/σ values for each quadrat support the assumption that the genocline, obtained by use of the herbarium specimens, is essentially what one would expect to result from the equal diffusion of genes, and that other factors apparently are of negligible importance in introgression as far as these genotypes are concerned. In fig. 14, then, I believe that we may assume the strong influence of subspecies

interior in the western quadrats to be due to the selective superiority of the cordate-leaved Ozark population. The same factors may likewise be assumed responsible for the concentric modification of ∠B observed within *A. t. interior*.

VII. Discussion and Summary

Asclepias tuberosa, popularly known as "butterflyweed," is a species of herbaceous perennials distributed from Ontario to Sonora, and from Minnesota to Florida. The plants occur chiefly in colonies of from few to over a hundred individuals in a wide variety of habitat from near sea-level to about 6000 feet elevation. They are facultatively self- or cross-fertilized through insect agency, and disperse their comose seed by air currents.

Three subspecies comprise *A. tuberosa: A. t. interior*, centering in the Ozark plateau and extending to southern Ontario, the Rocky Mountains, and northern Mexico, *A. t. tuberosa*, centering in the southern Appalachian Mountains and extending to the Atlantic coast, and *A. t. Rolfsii*, which centers in Florida and extends onto the coastal plain of Alabama, Georgia, and the Carolinas. Since the subspecies apparently are quite panmictic and freely hybridize at the present time, it is assumed that they have had their origin in isolation on the Paleozoic and Early Mesozoic land masses, Ozarkia, Appalachia, and Orange Island, respectively.

The purpose of this study is to investigate the population patterns of the three subspecies, particularly with regard to their apparent introgressive hybridization. This is accomplished by the measurement of leaf characters, which provide the principal systematic criteria of the subspecies. Unfortunately, it is found impracticable to distinguish leaves of all three subspecies by means of a single continuous scale, so only those of *interior* and *tuberosa* actually are measured; information concerning the role of *Rolfsii* is obtained only indirectly in so far as it influences the other data. Measurement of median length and width is in millimeters, and of apical taper (∠A) and shape of base (∠B) in standard degrees of declination, according to a rather elaborate procedure. Leaves are measured from herbarium specimens and from natural colonies growing in the field. The former are considered to yield the best estimate of the natural parameters of the subspecies for various reasons.

From the herbarium data separate phenocontour maps are constructed for ∠A, ∠B, median length, and median width. Isophene systems are plotted to indicate gene flow between subspecies *interior* and *tuberosa* with respect to ∠A and ∠B, the two characters which best differentiate the populations from the systematic standpoint. In the map for ∠B, "crests of variability," indicative of maximum heterozygosity, occur midway of the genocline of *interior* and *tuberosa*, and also about midway between the centers of dispersal of *tuberosa* and *Rolfsii*.

In the maps for length and width, more or less conspicuous increase in leaf size is seen to be associated with the former "crest of variability," and this is interpreted as an indication of hybrid vigor. No heterosis is found to be associated

with the second crest, and neither crest of variability nor heterosis is associated with the genocline of ∠A. It is not practicable to draw isophenes for length and width, but both geoclines and ecoclines are observed, the latter apparently related to restriction of population size under the influence of selection pressure, particularly in the southwest. In all characters, the individual colonies behave as microgeographic races, which are combined variously to form the major population patterns.

One of the most interesting phenomena to be demonstrated is the concentric diffusion from the Ozark plateau of a special modification of ∠B which, because of certain associated selective advantages, appears to be supplanting the ancestral race. A crest of variability is associated with the diffusion of this character, which probably dates since the Pleistocene, but there is no apparent heterosis. For various reasons, it is interpreted as possibly due to a major change of genotype.

The close correspondence of the centrifugal modification of ∠B to Matthew's (1915) hypothesis of the centrifugal migration of primitive organisms is obvious. Although our data confirm the general thesis of Matthew, *viz.*, the peripheral distribution of the supposedly primitive forms, climate clearly is not an active agent in this case.

Analysis of natural populations suggests that ∠A and ∠B are due to multiple factor complexes between which there is slight linkage. Segregation apparently is Mendelian.

Introgression in the subspecies of *A. tuberosa* is believed to proceed from initial hybridization through back-crossing to other heterozygotes and both ancestral types, respectively, to produce a more or less perfect gradation of genotype. Gene flow from either ancestral type is thought to be facilitated by crossing-over to effect redistribution, and the velocity possibly may be dependent upon the distribution of genes, particularly with respect to loci. Velocity of gene flow is observed to be directly proportional to population density. Although gene flow may be equal in either direction, as in ∠A, associated selective advantages of one gene complex may inequalize the balance, as in ∠B. Gene flow may be inequalized also by factors mechanically influencing migration pressure, such as the direction of prevailing winds; this, however, probably is of minor importance in *Asclepias tuberosa.*

The most obvious evolutionary role of introgressive hybridization might appear superficially to be merely the negative one of the obliteration of previous specific or subspecific distinction. However, the resultant increase of potential variability may play an important part in subsequent systematic differentiation.

Introgression of *A. t. interior* and *A. t. tuberosa* appears to proceed more rapidly along roadsides than in undisturbed areas.

During my studies of *Asclepias tuberosa* I have been the grateful recipient of favors from a multitude of friends, unfortunately too numerous to mention individually. These unselfish people, widely distributed throughout this country, enabled me to continue the investigation of geographical variation during the war

years when extensive travel was impossible. To my colleagues Edgar Anderson, Richard Holm, and Harrison Stalker, I am particularly indebted for their generous attention, encouragement, and suggestions. I am quite sure that I would not have been able to bring my work to conclusion without the instructive companionship and loyal assistance of Mr. Holm.

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FIELD STUDIES OF GUATEMALAN MAIZE[1]

EDGAR ANDERSON

The variation pattern of *Zea Mays* is surprisingly like that of man It is made up of a number of poorly defined geographical races and sub-races, some of which characterize wide areas while others are of restricted distribution. The members of any one population vary greatly one from another, and ordinarily it is only by statistical methods that one can demonstrate regional differences.

In maize, as in man, there are centers of variation in which strikingly different forms are found in a comparatively small area. For the maize plant one of these centers is western Guatemala where, according to Mangelsdorf and Cameron (1942) "in an area less than half the size of the state of Iowa are found probably more distinct types of corn than occur in the entire United States." This great variability of Guatemalan maize has attracted numerous collectors and is one of the reasons why Iowa State College recently established a Tropical Research Center in Antigua, Guatemala. However, judgments with regard to the comparative variability of Latin American maize need to be made with greater caution than they have been in the past. Most of the corn in the United States corn belt is uniform in color. Much Latin American corn has not been so rigidly selected for that feature and to our eyes looks more conspicuously variable than it really is. As every geneticist knows, a few segregating color genes can give the impression of great variability to a population which is relatively uniform morphologically. As we shall demonstrate below, Guatemalan fields are, morphologically, among the most uniform which have yet been studied, though there is indeed a great variation between different varieties.

Unfortunately, most of the collections of maize from Guatemala are of separate ears bought in the market or obtained at agricultural exhibitions, or bought from farmers. Maize, however, is a cross-pollinated plant and single ears are therefore not as significant as in some other crops. In wheat, which is almost continuously self-pollinated, a single spike, if well chosen, may be an efficient representative of that variety. In maize (extremely heterozygous and nearly always cross-pollinated under natural conditions) a single individual is somewhat of an accident. Out of all the millions of gene combinations which might have occurred in a particular field any single ear is one of the relatively few gene combinations which did come into existence. Unless carefully chosen it is not an efficient reflection of the gene frequencies in the field where it was grown. Were it selected to be representative it might have more significance but, as Cutler (1946) has recently shown, the very

[1]This work was made possible by a special grant from the Pioneer Hi-Bred Corn Company and Dr. I. E. Melhus, Director of the Iowa State College Tropical Research Center, who kindly made available the facilities of his laboratory during my stay in Guatemala. I am also indebted to the Office of Foreign Agricultural Relations and to Director Antonio Goubaud Carrera, of the Instituto Indigenista Nacional of Guatemala, for many favors.

reverse usually takes place: it is the unrepresentative ear which is odd-looking and gets the attention of the collector. Cutler has actual statistics on this point and they are impressive (loc. cit., p. 261):

> In the case of maize, colored or freak ears frequently receive more attention than normal ones. For example, in a harvest of 8000 ears at Santiago de Chiquitos, Bolivia, only four ears differed from the predominating type, yet in a collection representing this lot, three of the atypical ears were included and only four of the major type.

There is a further reason why collections made in the market place may not be at all representative. Some of the most distinctive and significant types of maize do not come to the market on the ear and have been missed by collectors. Through most of Latin America there are old-fashioned types of corn which seldom or never appear in the markets but which are used for particular purposes, most of them survivals of pre-Columbian practices. Three examples of such specialty corns are popcorns, brewing corns, and sweet corns.

Popcorns are very widespread in Latin America. A glance at the ethnological and agronomic literature will show that they have been obtained by very few collectors. This is largely because, if marketed at all, it is the popped corn which is sold, usually in various sweetmeats, while the ears do not generally appear. Brewing corns are widely distributed; how widely we cannot say for certain until careful collecting has been done. Since in many places brewing, though common, is illegal, it requires tact and experience and persistence to obtain ears of such varieties. Sweet corns (i. e., maize with one or more of the recessive genes for sugary endosperm) are widespread in Latin America. They are seldom used for green corn as in the United States. They were apparently pre-Columbian sugar sources and have survived in the manufacture of certain distinctive beverages and sweetmeats. They are known in Mexico, Guatemala, Peru, Ecuador, Bolivia, and from the Hopi Indians in the United States. In most of these places the ears are not commonly sold in the market, and it is only through careful field studies that we shall be able to map their present extent and trace their probable history.

For the above reasons the maize samples reported on in this paper were taken from fields, from drying floors immediately after harvesting, or from the cribs *(trochas)*[1] where the maize was being stored. In so far as possible they are random samples of 25 ears from each field. When for any reason they do not represent such a sample the fact is so stated in the Appendix. In making selections from a field the two or three outer rows of plants were avoided as being unrepresentative. An ear was taken from a randomly chosen plant in any one row, from the fourth plant in the next row, from the eighth in the next, and so on diagonally across the field until 25 were secured. In making crib or drying-floor selections the calipers were thrown out onto the surface of the ears and the ear nearest their tip was chosen for measurement. However, nubbins and poorly filled ears were of necessity rejected. It may be well to discuss the reasons behind this decision. In the part of Guatemala where these studies were made, as in most of the United States, each normal plant bears one perfect ear, though all the nodes below the one bearing

[1] Guatemalan spelling of "*troche*."

the ear are also potentially fertile. In a small percentage of cases one or more of these lower nodes bears an imperfect ear, as do so also occasionally the axillary shoots from the base of the plant (the "tillers" or "suckers"). Most of these small, imperfect ears can be recognized at a glance by an experienced person. In the United States they are called "nubbins"; in Guatemala, "mulco" is the commonest name in the Antigua region. To have included measurements of them with measurements of the upper ear would almost be like including a few leg measurements with arm measurements when studying a human population. The imperfectly pollinated ears are rejected because their kernels do not develop normally and measurements, such as width of kernel, would be almost meaningless.

It may also be well to discuss the actual way in which the collections were made and the measurements obtained. During the long dry harvest season in upland Mexico and Guatemala it is a simple matter in almost any town to find a field which is being harvested or a patio or drying floor where maize is spread out to dry. If the town is Spanish-speaking a request at the gate is almost never denied, particularly if one explains that he does not wish to buy the corn but merely wants to study it. Once permission is obtained one sits down by the corn (or actually on it in the corn crib) and measures his sample of 25 ears. This takes from one to two hours depending upon interruptions. (A pocket full of hard candies to pass out to the children of the household is almost as indispensable as a sliding micrometer.) After the 25 ears have been measured a few of them are photographed, and then one courteously takes his leave. This process is so simple that one can scarcely dignify it with the name of a technique and yet it is of real importance in taking efficient samples of Latin American maize and interpreting the results of such sampling. It is time-consuming but the time is well spent. For the first few moments most of the family stands around watching, and then the spectacle of a strange foreigner carefully measuring ears of the corn becomes dull, even for a Latin American family, and the normal life of the household begins to go on its usual way. Life in such homes is centered about the patio and as one sits there busy with the corn, he learns, incidentally and in a painless kind of way, a great deal about the family who owns the corn. When the men have gone back to work the old grandmother of the family will enjoy discussing the ways in which corn is made for food in her family, and frequently she can supply information about brewing corns or popcorns that cannot be obtained from local agronomists or corn merchants.

Maize is a sensitive mirror of the people who grow it. It is so highly heterozygous that good or bad management and careful or careless selection leave their imprints upon the character of the population. There are so many kinds of corn and they are so different and yet cross so readily that the introduction of alien sorts leaves a permanent witness of the mixture. One cannot interpret population samples of maize efficiently without understanding as much as possible about the people who grew that maize. The long, dull hours spent in measuring the samples of maize yield a priceless harvest of understanding.

The actual results from the Guatemalan studies are presented in Table I and also in the Appendix. The characters measured have been described and discussed in full in "Maize in Mexico" (Anderson, 1946). This discussion need not be repeated here, other than to point out that the characters were chosen after preliminary studies in the field and in the experimental plot. The scatter diagrams used in the Appendix attempt to present a picture of the population sample in one simple, easily grasped diagram. As explained in the introduction to the Appendix, the scoring of kernel texture[1] has been made more objective since "Maize in Mexico" was published. It is now scored in 6 grades as follows:

0. No soft starch at apex of kernel
1. Soft starch but no denting
2. Soft starch and a small dent
3. Soft starch and a deep dent but no wrinkling of the pericarp.
4. Soft starch and wrinkling pericarp
5. Soft starch and the apex of the kernel collapsed

In Guatemala, even more than in this country, the kernels at the tip and the butt of the ear are often different from those in the middle portion. The scores for kernel characters attempt to reflect the average condition of the middle third of the ear.

Through the courtesy of the O.F.A.R. it was possible to make an experimental test of the reliability of the methods of sampling and measurement used in these studies. At the experimental plot at Quezaltenango a common yellow variety from Salcajá had been used in a series of fertilizer test plots. Numbers 1 and 2 in the Appendix show the result of sampling the untreated plot and that to which phosphorus and nitrogen had been added. A random sample was taken from each as it was drying after harvesting, and photographs were made of the corn as it lay out in the sun. As shown in the Appendix, there are only very slight differences between the two samples by the methods used in this study. Maize is so variable and is so visibly affected by differences in soil fertility that I have frequently been asked by agronomists as to how much confidence could be placed in my 25 ear samples. Since the standards by which these sampling methods had been developed are essentially those of most taxonomic work it has been difficult to give an intelligible answer to those unacquainted with taxonomic practice. Though they seldom put it in words, taxonomists learn to choose characters which are relatively stable under environmental variation.

My general approach has been to work out methods of sampling and to choose characters for study which would give consistent results for repeated sampling of the same field, or for different samples of the same variety, and yet were efficient in distinguishing between varieties which were manifestly different. The methods have been used with increasing confidence when they demonstrated the regional

[1]See Anderson & Cutler (1942) for a discussion of the reasons for abandoning "flour," "flint," and "dent" as special texture categories in Central America.

TABLE I

FIELD AND CRIB COLLECTIONS OF GUATEMALAN MAIZE*

Region	Locality	Kernel denting	Ear width (mm.)	Shank diameter (mm.)	Number of rows	Kernel width (mm.)	Number of ears measured
Antigua	San Antonio Aguascalientes	0–1–3	40–50–57	9–17–23	10–14–18	8½–10½–12½	25
	Recolección, Antigua	0–2–4	44–49–59	15–22–31	12–16–18	8½– 8½–10½	25
	Medio Monte	1–1–3	43–47–55	12–17–20	12–14–18	8½– 8½–10½	25
	Dueñas	0–1–3	40–49–52	14–19–26	12–14–18	8½–10½–10½	25
	Dueñas, P. Alegría	0–1–3	45–49–57	13–20–26	10–14–16	8½–10½–12½	25
	C. Vieja, Rosario	0–1–3	47–54–64	12–22–34	14–14–18	8½–10½–12½	25
	C. Vieja, Montañes	0–1–3	44–59–63	14–23–36	12–14–16	10½–10½–12½	25
Sacatepeques	Santa Lucía (amarillo)	0–1–3	36–43–51	12–19–25	8–10–16	6½–10½–12½	25
	Santa Lucía (negrito)	0–1–3	38–43–49	11–16–25	10–10–14	8½–10½–12½	25
	Santa Lucía (blanco)	0–1–2	41–46–52	14–21–28	8–12–14	8½–10½–12½	25
	San Juan de l'Obispo (am.)	0–1–3	41–45–55	11–19–27	10–12–14	8½–10½–12½	25
	San Juan de l'Obispo (neg.)	1–2–3	45–53–60	14–21–33	10–12–16	10½–12½–12½	25
	San Lucas (pinto)	1–1–3	39–43–52	13–19–24	10–12–16	8½–10½–14½	25
	San Lucas (amarillo)	0–1–4	32–39–45	11–15–25	8–10–12	8½–10½–12½	25
	Mixco, A. Castillo	1–1–3	33–42–51	10–20–24	10–12–18	8½–10½–14½	25
Plan de Paramos	Chimaltenango	1–2–3	38–44–55	9–15–20	10–12–16	6½–10½–12½	25
	Paramos (above)	1–2–3	42–45–54	10–14–20	10–12–18	8½–10½–12½	25
	Paramos	1–2–3	43–53–62	17–21–27	12–14–20	8½–10½–14½	25
	San Miguel Morazón	1–2–3	38–42–47	11–16–19	8–10–12	10½–10½–12½	13
Quezaltenango	Salcajá (unfert.)	0–2–4	36–42–48	9–14–19	8– 8–12	10½–12½–14½	25
	Salcajá (fert.)	1–1–3	35–39–49	8–12–19	8– 8–12	10½–12½–14½	25
	High above Zuñil	1–1–2	40–47–51	12–18–27	10–12–14	8½–10½–14½	11
	Above Zuñil (yellow)	0–1–2	39–42–47	11–16–21	10–12–14	8½–10½–12½	25
	Above Zuñil (white)	0–2–3	39–49–56	9–17–25	10–14–18	8½–10½–12½	25
	Nueva Cuartel (white)	1–3–4	41–49–59	5–15–21	12–16–22	6½– 8½–10½	25
	Nueva Cuartel (yellow)	0–2–3	37–43–52	5–14–23	8–12–14	8½–10½–12½	25
	Doña Laura (white)	1–3–4	38–44–50	8–13–19	10–12–16	6½– 8½– 8½	25
	Doña Laura (yellow)	1–2–3	28–36–41	7–11–16	8–10–12	8½– 8½–10½	25

* For each character, the lowest value is given, followed in succession by the average for the collection, and by the highest value. At San Antonio Aguascalientes, for example, the lowest number of rows of kernels on any ear in the sample was 10, the highest was 18. The average value (median) for the collection was 14.

differences of Mexican maize, and the gradual transition from one region to another. However, these are essentially taxonomic judgments and they are not convincing to most agronomists. It is gratifying, therefore, to present experimental data on this point. As can be seen from the photographs, the Salcajá maize differs markedly in yield and vigor and in percentages of imperfect ears under the two treatments. Random selections of well-filled ears, however, yielded two similar samples from the two plots. This is a demonstration of the fact that the characters we have chosen for measurement have a strong germinal basis and that under conditions which will produce approximately normal plants they are not greatly affected by soil differences.

The 30 collections presented in Tables I and II and in the Appendix are from three nearby regions, all in the highlands of Guatemala. Seven are from the Antigua basin at elevations of about 5000 feet. Twelve are from plateaus near Antigua but from 500 to 1000 feet above it. Of these 12, 8 are on the San Lucas plateau or just below it, while 4 are from the Chimaltenango region. Nine samples are from Quezaltenango, a little over 50 miles to the northwest of Antigua and 1000 feet higher.

TABLE II

COMPARATIVE VARIABILITY OF MAIZE COLLECTIONS FROM GUATEMALA AND FROM WESTERN MEXICO

Maximum number of ears (per 25 ear sample) with same row number and kernel width.	5	6	7	8	9	10	11	12	13	14	15	16	17
Guatemala (29 samples)	2	4	3	4	2	3	2	4	1	2	0	1	1
Western Mexico (29 samples)	5	7	3	7	2	3	1	1	0	0	0	0	0

Although the numbers of collections are small, two generalizations can be established from the facts summarized in Table I. Both of them find further confirmation in the Appendix: (1) For the characters measured there is a general trend with altitude for most of the characters. From Antigua (5000 feet) to the plateaus above it (5500 feet), to Quezaltenango (6000 feet), the ears become generally smaller, with smaller shanks and fewer row numbers. (2) Differences between varieties are greater in the Quezaltenango region.

One quite unexpected fact is demonstrated over and over again in the Appendix. Much of the common maize in Guatemala is highly uniform. As will be shown below, there is indeed great variation in type in certain parts of Guatemala, as Mangelsdorf and Cameron pointed out. It is all the more surprising, therefore, to report that in many fields and even within certain regions, the plant-to-plant variation of *Zea Mays* is less than in any other region we have studied, including even the highly selected open-pollinated varieties of the United States corn belt! This is particularly striking in the Antigua region, but the same general tendency

Text-fig. 1. Popcorn balls (some of them wrapped in corn husks) being offered for sale by an Indian woman (upper left) in the market at Patzún, December, 1946.

Text-fig. 2. Corn just brought in from the field, drying in the yard of an Indian home in San Antonio Aguascalientes. Note its uniformity to type.

3

4

Text-figs. 3 and 4. Corn in the drying yard of a non Spanish-speaking Indian above Zunil. Superior and uniform ears laid out to the right (close up in the lower picture) are apparently being saved for seed ears. Note that a few ears with red pericarp are being deliberately included with the white ears, a very widespread practice in the New World among primitive peoples.

will be found to run throughout the collections. It is particularly striking when the scatter diagrams of the Appendix to this paper are compared with those in the report on Mexican maize.

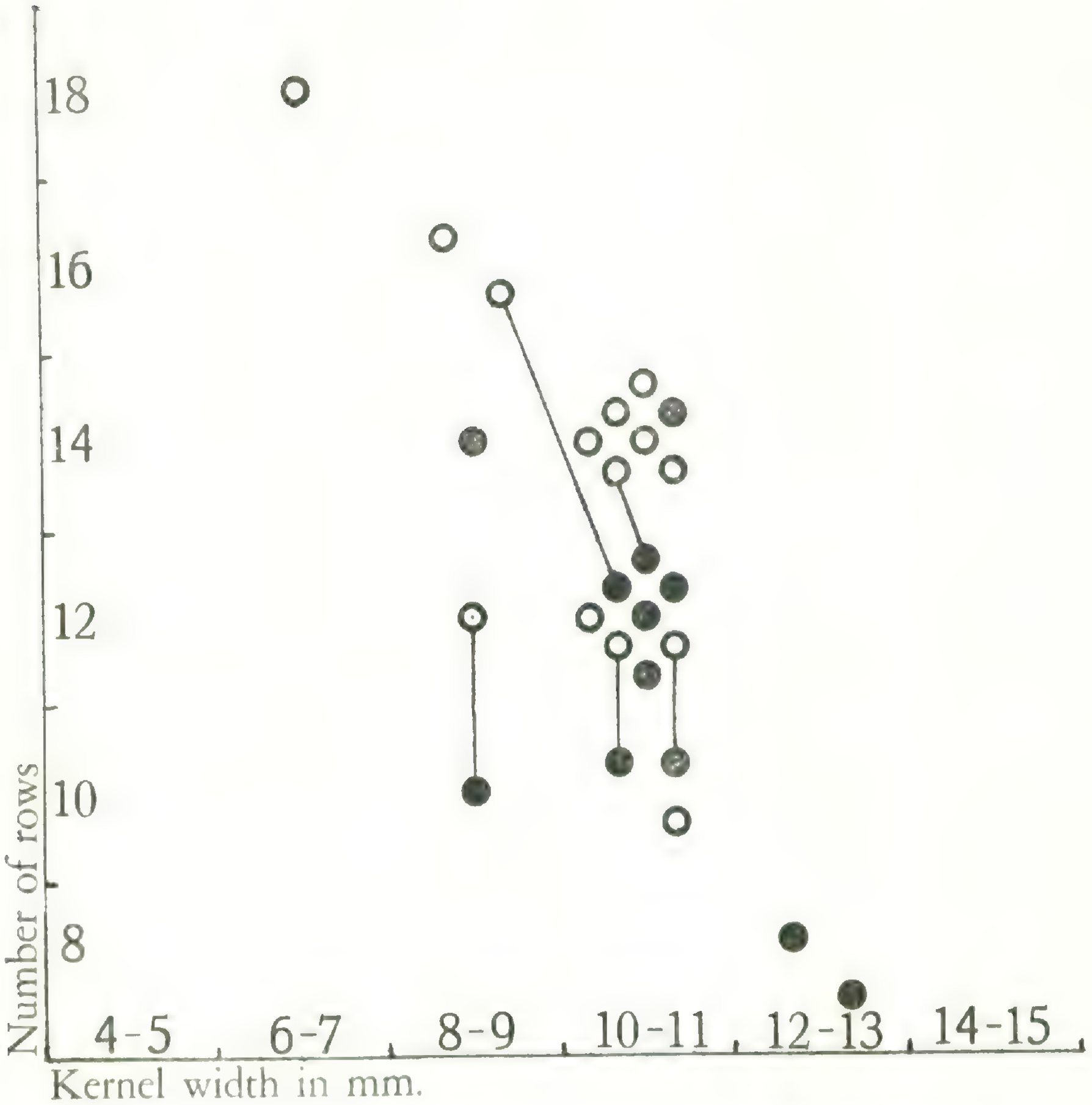
The maximum number of specimens for one of the cells on the scatter diagram is presented in Table II for the 29 Guatemalan collections which had 25 ears each. It is contrasted with a similar summary of the first 29 such collections in the Appendix of "Maize in Mexico." It will be seen that while the Mexican maximum varied from 5 to 12, the Guatemalan maximum went up to 17. The average (median) value of the cell maximum was 7 for western Mexico and 9 for Guatemala. Yet the Mexican collections were made in an area where there are strikingly fewer types of corn per 100 square miles than in the Guatemalan area.

Four of the collections from the Antigua region have from a half to two-thirds of the sample falling in the same cell of the scatter diagram, which means that they have the same row number and do not vary more than one millimeter in kernel width. Somewhat of the same stability is shown when we make comparisons between varieties in the Antigua region. Of the 25 ears each, of the 7 samples, 68 (or just over one-third) fall in the same cell (14-rowed, 10–11 mm. width of kernel) on the scatter diagram.

The reasons for this stability of Guatemalan maize require further study. In part, at least, they rest upon a rigid selection for physical type in picking seed ears. Among pure-blooded Indian farmers maize is often very carefully selected for type. Figure 3 shows the maize drying floor of an Indian family living on the slopes of a volcano above Zuñil. The family was not Spanish-speaking, and those remaining at home fled when we approached. However, as shown in the photograph, some of the best ears had been segregated at one side of the pile. They are obviously seed ears for next year. The rigid selection for type is about on a par with that practiced by farmers of the United States corn belt in the days before "hybrid corn" when most farmers selected their own seed ears.

Of the 11 samples of white corn 6, as shown in fig. 4, had their averages in the same cell of the scatter diagram, with row numbers of 14 and kernels 10–11 mm. wide. It represents a common, well-marked type in the Antigua region where it was seen repeatedly in markets and being packed to market, on drying floors and in the fields. It has (pl. 47, left) an ear of about the same size as United States cornbelt varieties, slightly enlarged at the butt, tapering gently to the tip, usually straight-rowed except for the enlarged basal portion, and very commonly 14-rowed.

As shown in fig. 5, the yellow corns of the same region are fewer-rowed on the average. They too represent a common, widespread type, particularly at higher elevations. On the highlands between Sololá and Totonicapán they represent nearly all the field corns of that area. They are most commonly 8- to 12-rowed, with an even more strongly marked enlargement at the base of the ear than in the white varieties.



Text-fig. 5. Averages of the field and crib samples of yellow and white corn made in Guatemala. Each circle represents the average value for number of rows and for width of kernel of a whole sample of corn from one field. Open circles denote white varieties, solid circles, yellow varieties. It will be noted that the white varieties on the whole have narrower kernels and higher row numbers. In five instances the same farmer was growing both a yellow corn and a white one. A narrow ruled line connects the two varieties in each of these cases. It can be seen that in each of these the white variety had a higher row number than the yellow variety with which it was associated.

In four of the examples in the Appendix (San Lucas, Santa Lucía, Doña Laura, Nueva Cuartel) and in an additional small sample from Jocotenango we have yellow and white varieties grown by the same farmer, or grown in an adjacent field. These five cases are diagrammed in fig. 5. It will be noted that in each instance the yellow variety has a lower row number than the white variety being grown with it. Though some of the yellows have as many rows as some of the whites, the white varieties being grown in those localities had even more.

These facts suggest very strongly that two of the basic elements in the maize of the Guatemalan highlands are a many-rowed white corn and an 8-rowed yellow corn. Though a great deal of mixing has gone on between them, and still continues, the white varieties, on the average, are larger-eared and with more numerous rows, the yellow varieties smaller-eared and fewer-rowed.

Even within the small area sampled by these field studies it is possible to demonstrate Mangelsdorf and Cameron's center of variability in northwest Guatemala. The 8 collections made in the Quezaltenango area are distinctly more variable among themselves than those from in and around Antigua. This is equally true whether one considers single characters (Table I) or the general over-all impression of the ear (Appendix).

Our data are not extensive enough either to prove or disprove Mangelsdorf and Cameron's thesis that this Guatemalan center is connected with the presence of *Tripsacum* and teosinte in the same general area. We have new information on only one point. The commingling of types is not necessarily the resultant of isolation into mountain valleys as they suggest.

Three of our collections were made within sight of each other, on one mountain slope, yet they are very different types of corn. Two of them were from fields belonging to the same family. It may be significant that these 3 collections were made on volcanic slopes above the Samalá River, which has been since pre-Columbian times one of the easiest approaches[1] from the coast into the highlands. Yet it is in this same area that varieties most like those of central Mexico are encountered. They have the sharply tapering ears, and the pointed kernels which characterize the common varieties of the Mesa Central.

It may be, as Mangelsdorf and Cameron suggest, that the conspicuous variability of the maize of northwest Guatemala is due to the actual commingling there of *Tripsacum*, *Euchlaena*, and *Zea*. On the other hand, from the available facts one could argue quite as well that Guatemala is a center where diverse strains of maize, which were differentiated elsewhere, met and hybridized. Nor are these two hypotheses mutually exclusive; it may be that the extreme variability of the maize of Guatemala is in part due to very different varieties from South America and from Mexico having met and hybridized at that point, and in part due to distinctive qualities acquired there by introgression from *Tripsacum*. These are questions which cannot yet be answered until we have reasonably complete population samples of Guatemalan maize.

If teosinte originated in the highlands of Guatemala as Mangelsdorf and Cameron suggested, and has there introgressed most extensively with maize, we might expect to find the maize of that area strongly tripsacoid in character. From the published accounts of Corn × Teosinte back-crossed with corn we might expect to find a high percentage of varieties more or less long-eared and few-rowed, with tapering, appressed ears. They would be borne on tough, narrow-leaved, slender-

[1] See McBryde (1947), footnote page 10.

stalked plants with strong root systems. Such varieties seem to be absent in the highlands of Guatemala but they do characterize wide areas in western Mexico. In the deep *barrancas* of western Mexico *Tripsacum* grows in variety and in profusion. It is there that the Tarahumare Indians are known (Lumholtz, 1902) to interplant maize and teosinte to introduce drought resistance and flavor to the former. It is there that *maiz chapolote*, a coffee-brown popcorn, one of the most tripsacoid of maize varieties, is and was commonly grown as a staple.

The varieties of the Guatemalan highlands often possess the low row numbers to be expected from teosinte but they combine the character with wide seeds, a large and differentiated butt, and a thick shank. The origin of these two latter characters is difficult to explain on any hypothesis. They reach greater extremes in Guatemala than in any other area known to me and characterize most of the maize of the highlands. This is particularly apparent when Guatemalan collections are compared with those from Mexico. This can be demonstrated when ear base outlines traced from photographs are compared for Guatemala, western Mexico, and central Mexico. The slight increase in diameter demonstrated in such photographs tends to be accompanied by changes in kernel rowing and even in kernel shape, as can be seen in the Appendix to this paper.

It is difficult even to suggest how such enlarged ear bases might have originated. Perhaps they came from crosses between cylindrical-eared varieties and short-eared, globular types like those of the Andes. They are altogether lacking in the extensive collections of prehistoric maize from western South America. They are developed only to a minor extent in present-day Andean varieties. They are not found over wide areas in Mexico, and in the few cases where they are highly developed (Chiapas, Mountain Yellow) it is fairly obvious that they have spread from Guatemala.

Their behavior in crosses indicates a multigenic basis, and it is difficult to see how they could have originated out of pre-existing maize varieties even by strong selection. There is no transparent reason why they might have originated by hybridization with *Tripsacum* or teosinte. It may be that they are in some way a recombination of genes from South American and Central American maize and that they are most strongly developed in Guatemala since it was there that mixtures of these two diverse stocks took place on a wider scale than elsewhere.

However these enlarged bases may have originated, their occurrence outside of Guatemala is an almost certain indication of a greater connection with the maize of that region. They are well developed in eastern North American flints (Brown and Anderson, 1947) and are only one of several characters which those varieties have in common with Guatemalan varieties.

More precise cytological and histological tests are under way. The "Mountain Yellow" varieties reported from Mexico also show obvious Guatemalan relation-

ships. In the American Southwest, where the prehistoric record has been most completely analyzed, enlarged bases appear suddenly in Pueblo III (Carter and Anderson, 1945) and have characterized the region ever since. Carter and Anderson referred to these Pueblo III long-eared corns as "Eastern" because of their close resemblance to Eastern American flints. There is as yet no evidence concerning the immediate center from whence they came. Whether it was from Mexico, or from eastern North America, or from the Great Plains, it is probable that ultimately, by some route, they trace back to Guatemala.

POPPING AND BREWING VARIETIES

These have been almost universally neglected by collectors. Mangelsdorf and Cameron list one popcorn and no sweet corns. McBryde (1947) mentions it only from Patzún. The Russian Expedition lists none of either type. Stadelman (1940) lists one sweet corn, and none of these authorities make any mention of varieties used for brewing. Though I was not able to study field samples of any of these special kinds of maize, I did collect a few ears. It seems probable that such varieties are fairly common in Guatemala. Since this statement will be received with almost equal skepticism in the United States and in Guatemala, it may be well to discuss the probability in detail. The explanation is of greater importance because the situation is not limited to Guatemala but is quite general in many parts of Latin America.

Certain distinctive types of maize continue to remain unknown because they are grown by non Spanish-speaking Indians ("indigenas"). These distinctive varieties are either used exclusively by the "indigenas" or are manufactured into products which do not readily betray their origin when they appear upon the market.

The gulf between the "indigena" and the "ladino"[1] is much greater in Guatemala than one might suspect from casual observation. The "indigenas" make up the bulk of the population. They are common everywhere, even in the capitol city, and many of the "ladinos" show unmistakable evidence of considerable Indian ancestry. It is not until one begins to investigate customs or products which are peculiarly Indian that he finds out how completely these two kinds of people go their separate ways, and how little one knows about the other. A woman from an Indian town may come into market regularly for most of her adult life but beyond the few words used in buying and selling she will have no knowledge of Spanish. A ladino family may live in a largely Indian village for generations and deal in agricultural produce, yet have little knowledge of those Indian food crops which are not brought to market. My understanding of this phenomenon is the result of efforts to obtain Guatemalan varieties of popcorn for study. It may be worth while to describe these in some detail, since they illustrate the difficulties en-

[1] For a complete discussion of the terms "ladino" and "indigena" see McBryde (1947).

countered in getting a complete understanding of maize in Latin America, and explain why certain very important types of food plants are still almost unknown to science.

I went to Guatemala knowing that popcorn had been collected there at least once, and with a general picture of its distribution and importance in Latin America which convinced me that it must occur in Guatemala, at least in the back country. From Erwin (1934) I knew that a popping Amaranth was also being grown in southern Mexico. I had been successful, under the tutelage of Dr. Isabel Kelly, in finding popcorn in various parts of Mexico from which it had previously not been reported, and my command of Spanish was sufficient to discuss the matter with all the Spanish-speaking people I encountered.

During my first three weeks in Guatemala I got almost exclusively negative results, though I now know that I was sometimes within sight of mountain fields where popcorn was being grown. Various visiting American collectors, most of whom had been on the outlook for strange varieties of maize, knew nothing about it. The staff of the National School of Agriculture was similarly uninformed, though they had an excellent and detailed understanding of the field corns of Guatemala. American residents of Guatemala and Guatemalan farmers, merchants, housewives, and landed proprietors gave equally negative replies with the exception of Mrs. Mildred Palmer, a specialist in Guatemalan textiles, who has direct business connections with various Indian villages. She assured me that popcorn balls were very commonly made and sold in various parts of Guatemala, though she knew nothing about the varieties of maize from which they were made. The ethnologists of the Instituto de las Indigenistas knew little about the matter but were most cooperative in gathering further information. They were soon able to supply me with a single ear of popcorn from the Quezaltenango region and the advice to try making collections in the town of Patzún.

In Patzún I got in touch with the local corn merchant, a most intelligent man, who had a wide and accurate knowledge of the field corns of the region and a lively interest in varieties of commercial importance. He supplied the information that popcorn balls were sold on market days in Patzún and that they were made exclusively by the Indians from special kinds of maize. He knew little, however, about these varieties. He thought there were two different kinds but was not certain. He thought one had pointed kernels and the other not, but could give no further information. I then hurried over to the town market and found popcorn balls being sold by a number of Indian women, none of whom could speak more than a few words of Spanish. Through an interpreter I attempted to buy ears of popcorn or at least seeds of that variety. The women attempted to pass off seeds of ordinary field corn as the source of their popcorn balls. As can be seen from the photographs in fig. 1, the kernels in the popcorn balls are fully exploded and could not have come from any such variety of corn. In the short time before my bus departed, the best I could do was to purchase a small amount of a rather mongrelized popcorn and to arrange to have more authentic specimens purchased

and mailed to me. They proved to be a most interesting variety with phenomenally large kernels for a popcorn, but they pop uniformly well. The kernels are wide and quite thick, with no indications of a point, and have a translucent white endosperm. The ears are slender, with 10–12 rows of kernels. They are quite unlike any native or commercial varieties of popcorn known to me.

The popcorn balls from this market led to further information. They were immediately recognized by every one in the servant class (i. e., people of predominantly Indian ancestry) to whom I showed them in the town of Antigua. They are known as *alborotos* and are very commonly[1] brought into town during Lent by Indians from Patcicía, a town near Patzún. (See also McBryde, page 10). The landed proprietors of Antigua to whom I showed them had either never noticed them before or did not know that they were made of maize. One well-to-do "finquero" who makes journeys to Chicago and San Francisco every few years told me that these popcorn balls were made from a plant closely related to "nihau" *(Amaranthus)*! I have not yet been able to collect any considerable amount of popcorn from Guatemala but on two occasions (above Zuñil and above Sololá) I have seen fields of an extremely small-caned maize growing in good land next to fields of large maize. It must have been either a popcorn or a special variety used in brewing.

The difficulties encountered in collecting popcorn are magnified in getting examples of varieties used in brewing or information about their use. More than one kind of home-made alcoholic beverage is made from maize in Guatemala, but such manufacture is illegal and one has to have the confidence of his informant if much is to be learned. In the short time at my disposal I was able to determine that varieties with a blue aleurone were preferred for this purpose, since they were sweeter and smoother. I was also assured by a most intelligent "ladino" woman, who lived in a town largely composed of Indians, that they had certain highly prized varieties used in brewing their ancient types of beverages. It it highly probable that ancient varieties with sugary endosperm are still in existence in Guatemala and that they are probably used in brewing there, as in South America. Stadelman lists a single ear, and his description reminds one of the *maíz dulce* discovered by Kelly in western Mexico (1943).

For the above reasons it is evident that we still know little or nothing about some of the most interesting varieties of maize in Guatemala, and that it will require patience and very special skills to obtain a full understanding of these types. The effort is worth while, not only because such information will illuminate the history of maize, but because, singularly enough, it is among such specialty corns that useful genes for modern corn-breeding are quite likely to be found (see below).

[1] Though similar confections made from a popping Amaranth and a popping sorghum are even more common.

Salpor.—

Unfortunately none of the fields included in this survey was planted to the highly developed "Salpor" or Flour Corn. This is a large-kernelled variety of white flour corn which is commonly grown in parts of the Guatemalan highlands. Judging from samples displayed in several markets, a good deal of the maize sold under that name in Guatemala is extensively contaminated with other kinds of corn. It very closely resembles the "*Cacahuazintle*" flour corns of Mexico which were probably derived from it, and is quite similar to the highly developed flour corns of Andean South America from which it may in turn have been derived.

Multiplication.—

Cutler has recently described under this name a bifurcation of the spikelet pedicel which increases the kernel number in South American maize. In its lowest grades it is responsible for the extra kernels pushed in between the regular rows of 8- and 10-rowed varieties. With a higher degree of expression it turns 8-rowed varieties into 4 quadrants, within each of which the rowing is irregular and obscure. In its extreme manifestation it produces an ear in which the regularity of the rowing, as in the "Country Gentleman" sweet corn, is no longer apparent. Though these ears look superficially similar to "Country Gentleman," they owe their increase in kernel number not to the development of the aborted floret (as in "Country Gentleman"), but to a doubling of the entire spikelet.

Multiplication is a common phenomenon in Guatemala and from cursory observation is more frequent and more extreme at higher altitudes. Actual percentage frequencies were obtained for several of the collections and are presented in the Appendix (nos. 6, 9, etc.).

Practical Considerations.—

A number of different agencies in Guatemala are already concerned about the yields of Guatemalan varieties, and breeding programs are already under way to improve them. American agronomists, or Guatemalan agronomists trained in the United States, are prone to begin any improvement program along the lines which have proved so conspicuously successful in the United States. In my opinion, this is ill-advised. In the first place, the variation pattern of *Zea Mays* is wholly different in Guatemala from what it is in the United States. In the second place, the conditions under which it is now grown and under which it is likely to be grown in the near future are different there and here. Hybrid corn owes its superiority in the American agricultural picture as much to its uniformity as to its superior yield. Except on a few large plantations there is little prospect of growing Guatemalan corn with power machinery by mass-production methods. Under Guatemalan conditions, therefore, the uniformity of hybrid corn would be of no particular advantage. The other advantage of hybrid corn, extreme heterozygosity, might well be achieved in Guatemala by much simpler methods. The fields in the Quezaltenango area suggest that Mexican varieties with many-rowed, more or less

pointed kernels combine well with Guatemalan varieties. It would be a comparatively simple matter to select open-pollinated varieties of white Guatemalan maize and of white Mexican maize which combine well with each other. They could be grown and improved by mass-selection methods. If the maximum improvement was worth the time and expense they could then be carefully selected every five or six generations for their combining ability with one another, using a modification of the plan originally selected by Hull (1945) of Florida. These two elite white varieties, each increased as an open-pollinated crop, could then be interplanted and detasseled as is hybrid corn in the United States, producing first-generation hybrid seed for sale and distribution.

The probable usefulness of Guatemalan maize in the United States.—

Since maize is of even greater importance in the United States than in Guatemala, the extreme over-all variability of Guatemalan maize is of great potential importance to our agriculture. This does not mean, however, that Guatemalan maize varieties, as such, can immediately be used in the production of better corn for the United States. As agronomy advances and it becomes increasingly practical to breed for particular characters in maize, Guatemalan varieties should prove increasingly useful. Resistance to particular diseases, high percentages of unusual amino acids, kernel texture, insect resistance, sugar content, etc. are characters which might well be expected in one Guatemalan variety or another. Once located, it would be a comparatively simple matter to transfer any particular one to a commercial inbred line. Once they are so incorporated they may be used effectively in the production of commercial hybrids for the United States.

It should be pointed out that in any such discriminating corn-breeding program as that just outlined all Guatemalan maize is of potential importance. As a source of disease-resistant genes or of increased quantities of useful amino acids, some small-eared, small-kernelled variety from the mountains may be quite as useful to United States agriculture as the large-eared sorts of spectacular productivity. It is even possible that some of the out-of-the-way varieties may be more useful than the ordinary run of Guatemalan field corns. To be specific, the popcorns and brewing corns are extreme types morphologically; the chances are good that they may also be extreme in their chemical composition and their disease and insect resistance. For purely practical reasons, therefore, Guatemalan corns should be systematically and comprehensively surveyed without reference to their immediate usefulness as field corns. We need, in the first place, a general survey of what kinds of maize there are in the country, what their general morphological characters are (row number, kernel texture, etc.). Then we shall be ready to make a systematic survey of their chemical compositions, disease resistance, etc., and will know where to turn for the characters we need in United States corn breeding.

Summary.—

1. Field sampling of maize is contrasted with sampling at markets and fairs. The latter is shown to give an erroneous and incomplete picture of Latin American maize.

2. The advantages of personal contact with the families which grew the maize sample are described and discussed.

3. Experimental data are presented showing the relative stability under varying fertility of the characters used in this study.

4. The data from 30 samples from the highlands of Guatemala are summarized in tables, charts, and photographs.

5. Even within the small area covered by this survey it is possible to demonstrate that with increasing altitude there is a general tendency for smaller ears, smaller shanks, and fewer row numbers.

6. In spite of the great over-all variability of Guatemalan maize, intra-field variability (and to a lesser extent, intra-variety variability) is *less* than in any other area from which field samples have been taken (including open-pollinated varieties from the United States corn belt). In part, at least, this uniformity results from a rigid selection for type.

7. The common white maize of this part of the highlands is described and illustrated. It is of about the size of United States corn-belt maize, with ears slightly enlarged at the butt, tapering gently to the tip, and is very commonly 14-rowed. The yellow varieties of the same region are mostly fewer-rowed with an even more strongly developed basal enlargement.

8. Inter-variety variability was slightly larger in the Quezaltenango area and was extreme even between fields on a single mountain side.

9. In the light of these results, Mangelsdorf and Cameron's hypothesis of Guatemala as a center for teosinte introgression is briefly discussed. It is suggested that such introgression might have taken place in western Mexico rather than in Guatemala.

10. The difficulties of securing samples of popcorns and brewing corns are described in detail. It is shown that such kinds of maize may be common and still be outside the orbit of visiting scientists. One variety of popcorn is described and its distribution discussed.

11. The phenomenon recently named "multiplication" by Cutler is common in Guatemalan maize. Frequencies are reported for certain of the field samples.

12. The practical improvement of Guatemalan maize varieties is discussed, as well as the best ways to use Guatemalan maize in the breeding of varieties for the United States. It is suggested that for the United States corn belt, little-known and curious out-of-the-way varieties such as popcorns and brewing corns may be quite as important as Guatemalan field corns of spectacular productivity.

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Explanation of Plates 47 and 48

PLATE 47

Common varieties of corn in the Guatemalan highlands. A little less than natural size (note centimeter scale at the base).

Left: Typical ear of white corn from the region around Antigua. Note the slightly enlarged and differentiated base, the gently tapering ear, the flinty kernel with a conspicuous cap of soft starch.

Right: Typical ear of yellow corn from the highlands. This one was grown at Quezaltenango from seed obtained at Salcajá. The wide flinty kernels were deep yellow; some of them had a slight capping of soft starch. The enlarged base and the slightly irregular kernels are typical. One of the ears from Nos. 1 and 2 of the Appendix.

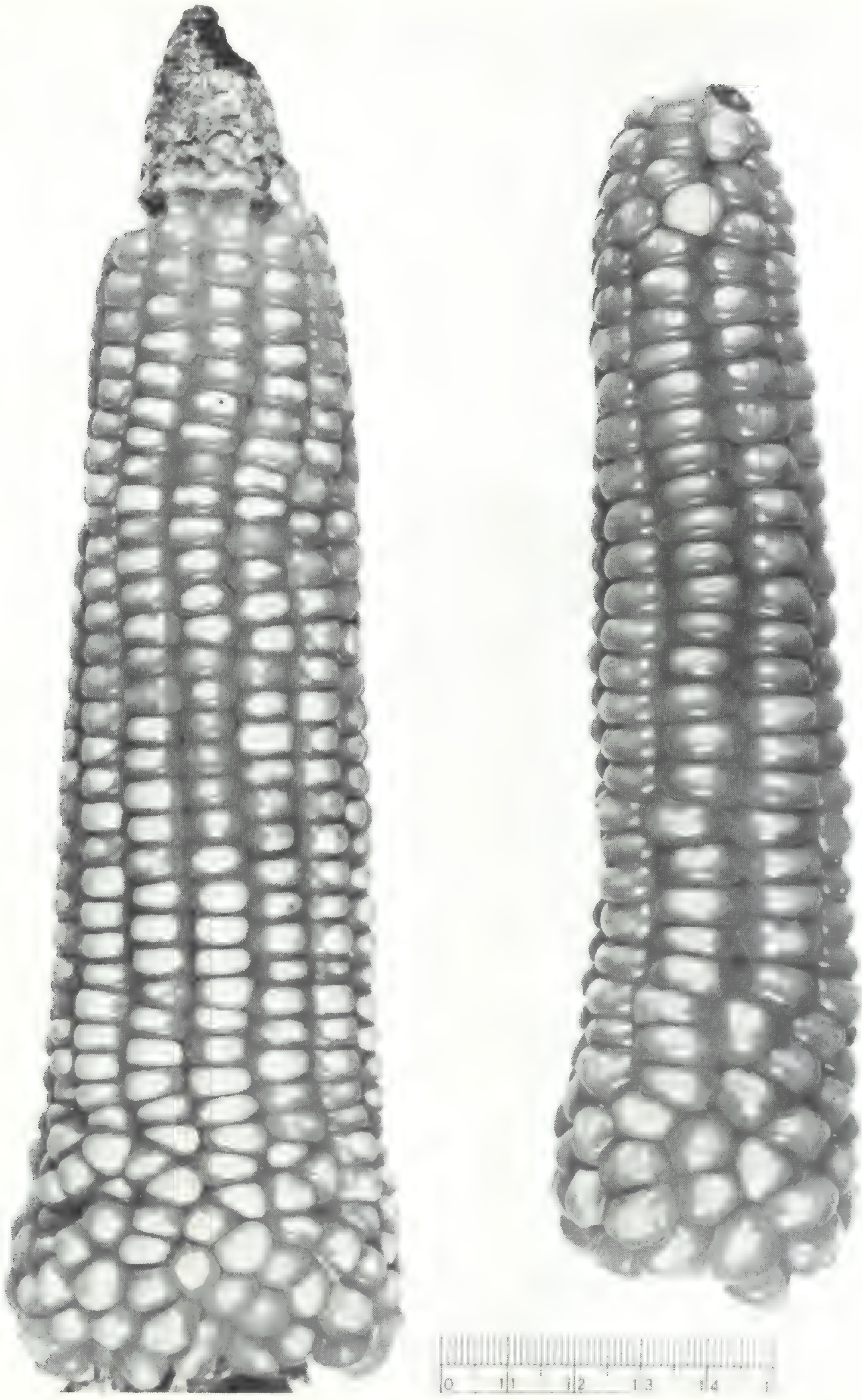
PLATE 48

Ears to the same scale as pl. 47

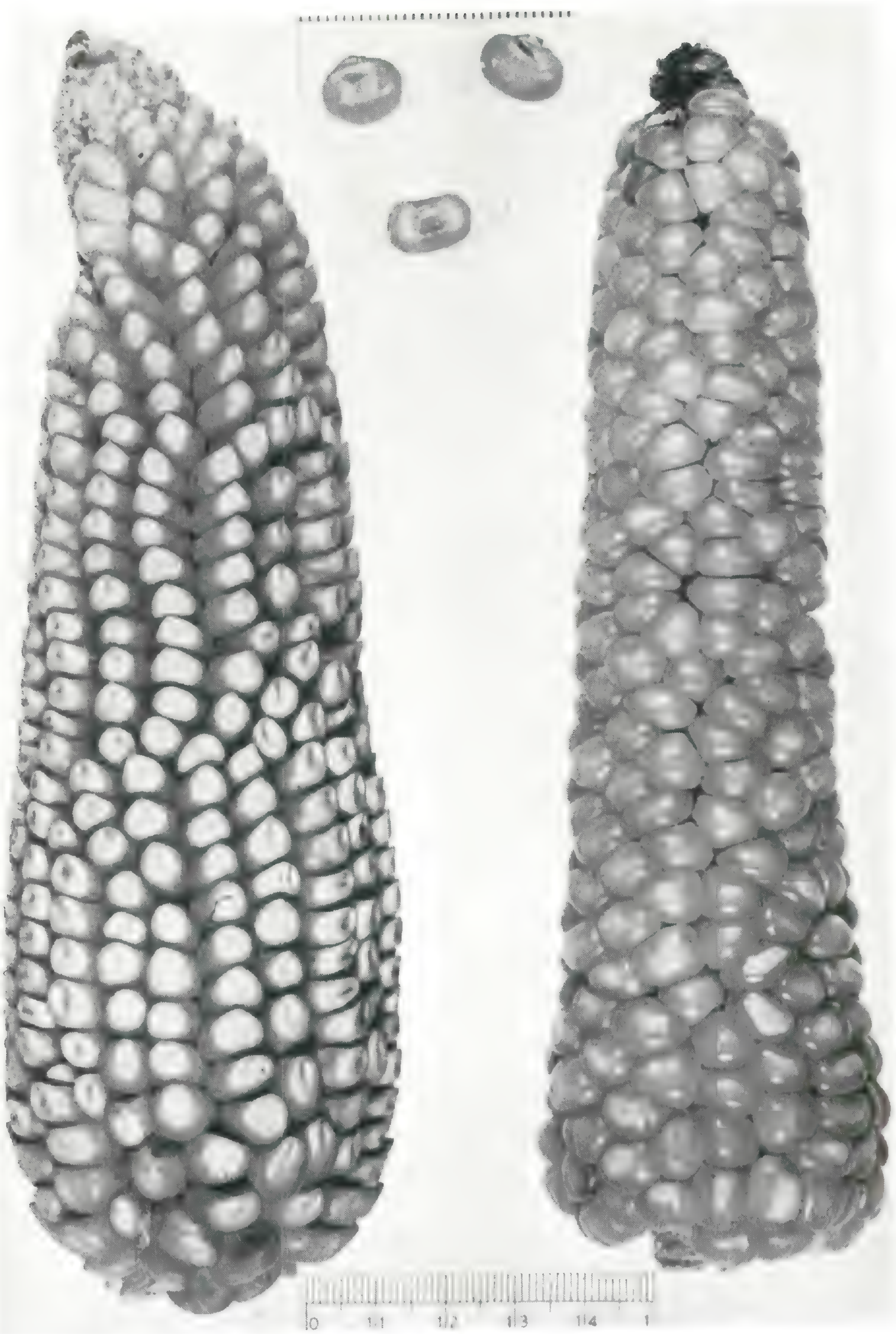
Left: Ear of white corn from Quezaltenango. In its high row number and pointed kernels this variety resembles the common corn of central Mexico. See No. 25 in the Appendix.

Insert: Kernels of popcorn from Patzún, slightly larger than natural size (note millimeter scale along the top edge of the plate).

Right: Ear of yellow corn from above Zuñil (see No. 23 in the Appendix). This is basically an 8-rowed variety with varying amounts of "multiplication." The ear illustrated here has so many extra kernels (due to "multiplication" in the sense used by Cutler, 1946) that the basic 8-rowed condition is almost impossible to follow.



ANDERSON—GUATEMALAN MAIZE



ANDERSON—GUATEMALAN MAIZE

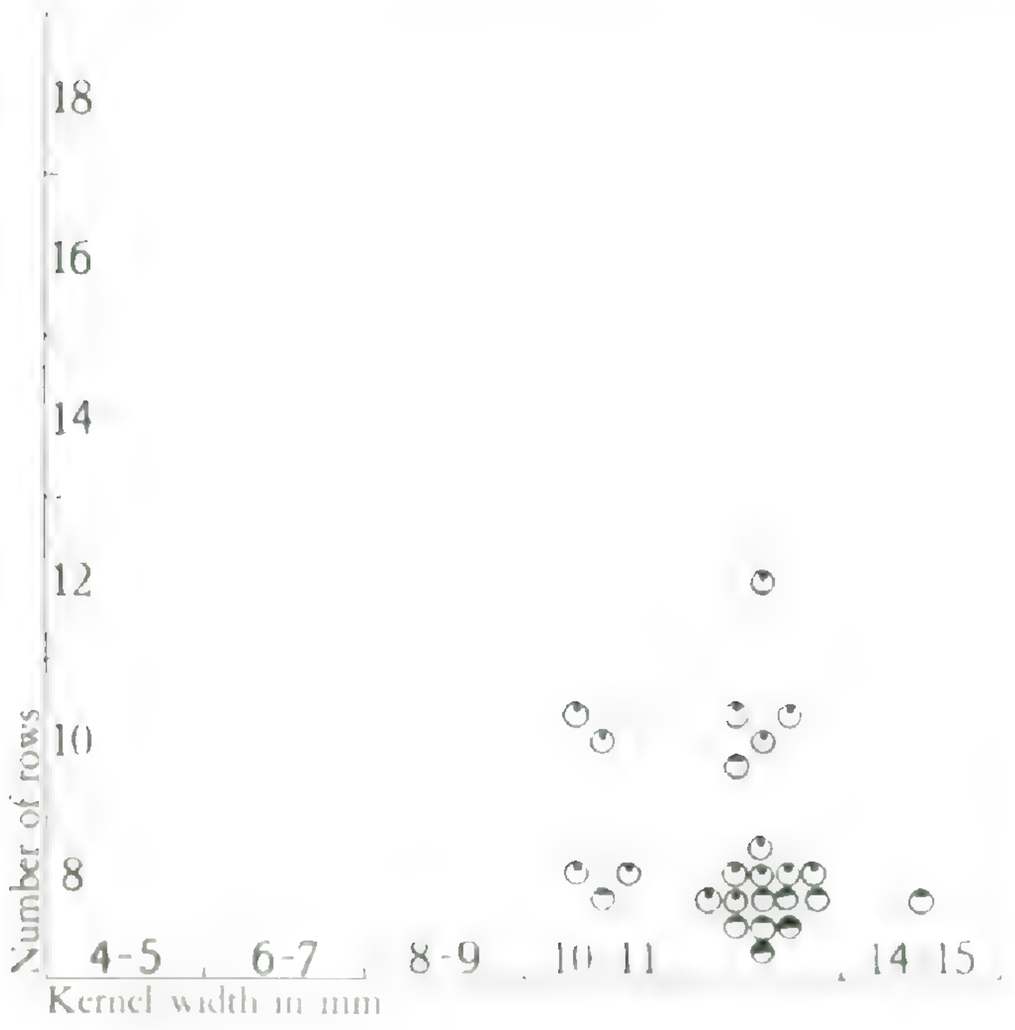
APPENDIX

The Appendix, in so far as space permits, gives a full presentation of the facts summarized in Table 1, along with other relevant data on variation. For many of the collections a Leica snapshot of a random sample of a few ears shows their general over-all appearance. These pictures are printed at approximately the same magnification. The sliding micrometer used in measuring the ears appears in each picture and can be used to make exact comparisons since it is set at 5 cm.

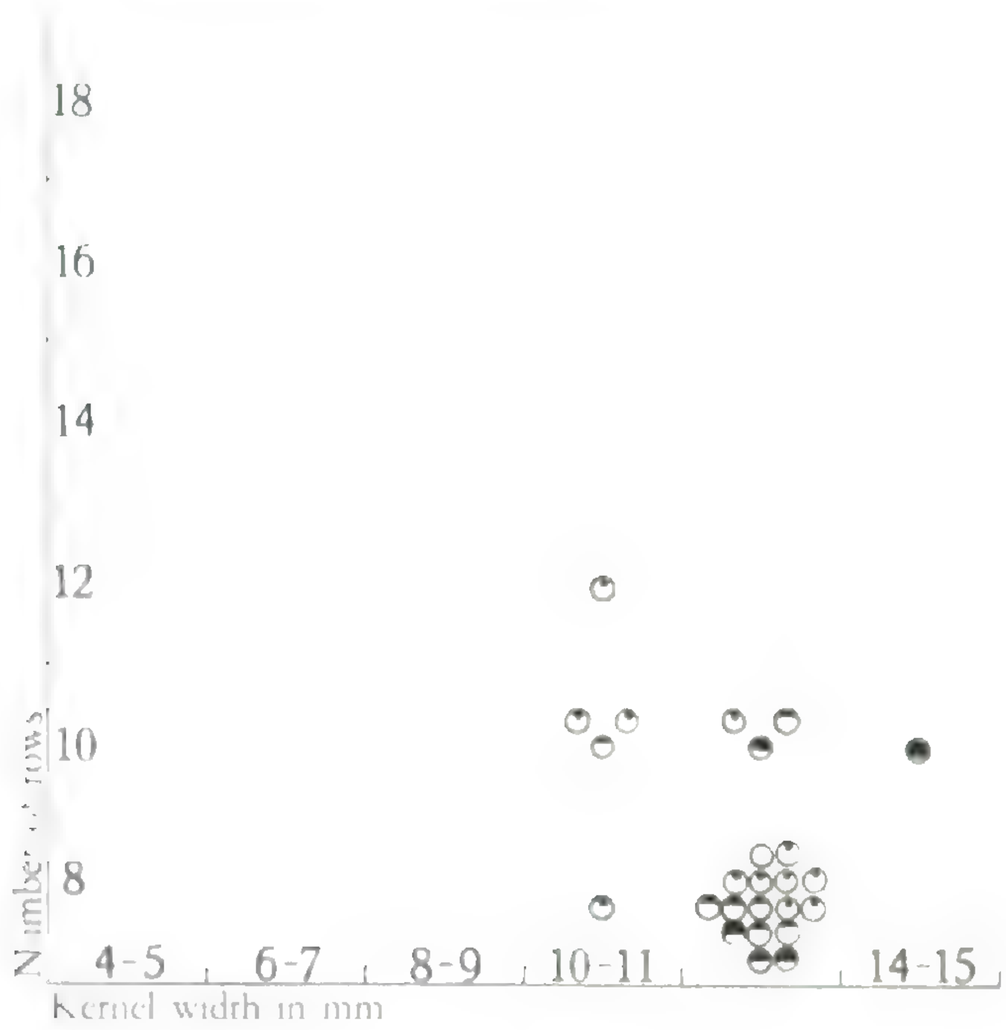
The population diagrams are of practically the same type as those used in "Maize in Mexico" (Anderson, 1946). While they look like correlation tables they are a much simpler device and are more like a scatter diagram; they are merely a way of showing graphically the kernel width, row number, denting of the kernel and pointing of the kernel of each of the ears in the standard 25-ear sample. Since each of these characters is a multiple factor character, and since each is at least partially independent of the other three genetically, the combination of all four provides a record of a good portion of the germ-plasm. The diagrams can be used as a record of what was growing at a particular place and time, as a means of making exact comparisons between varieties or between different fields of the same variety, or (analytically) to examine the effect of a certain variety on the morphology of others being grown in the same neighborhood.

Each little glyph (circular or pointed as the case may be) represents one ear of corn. Its shape denotes the shape of the average kernel on that ear (pointed, slightly pointed, without an obvious point); its color represents the texture of an average kernel. Texture was scored as follows: open circle, no soft starch at the tip of the kernel; open circle with a dot, cap of soft starch but no indentation of the kernel; upper quarter of the circle filled in, cap of soft starch leading to a small indentation of the kernel; upper half of circle blackened, so much soft starch that there is a deep indentation in the kernel but no fine wrinkles on its surface; upper three quarters of the circle blackened, a denting of the kernel plus fine wrinkles in the seed coat; entire black circle, soft starch deposition so extreme that there is a deep wrinkled dent in the tip of the kernel and it is more or less collapsed (this condition, though common in central Mexico, was rare in the part of Guatemala covered by these studies). In other words, the blacker the glyph, the greater is the amount of soft starch.

The diagram can be thought of as a set of pigeon-holes simultaneously cataloguing the ears with regard to their row number (upright scale) and their kernel width (horizontal scale). It sorts out the ears into a series of squares, and all the dots falling in each square represent ears having the same row number and kernel width. The glyphs are arranged in a standardized fashion around the center of each square; variations in position within each of these squares are of no significance. In one or two instances a bar at the side of the glyph is used to mark certain special ears (such as those reserved for seed, or nubbins, "mulcos", etc.).



1. Salcajá



2. Salcaja

1 and **2.** Common yellow corn from Salcajá. Photographs taken of the harvest at the O.F.A.R. plot at Quezaltenango. No. 1, from a plot fertilized with additional nitrogen and phosphorus; No. 2, the same variety from an adjacent unmanured plot. Though No. 1 yielded much heavier (note that grass is not visible between the ears as in No. 2) and had somewhat longer ears, their kernel type and row number were not affected. In both lots all the cobs were white, all the kernels had yellow endosperm, and there were no kernels with colored aleurone. In each sample of 25 ears, 12 showed multiplication.

1

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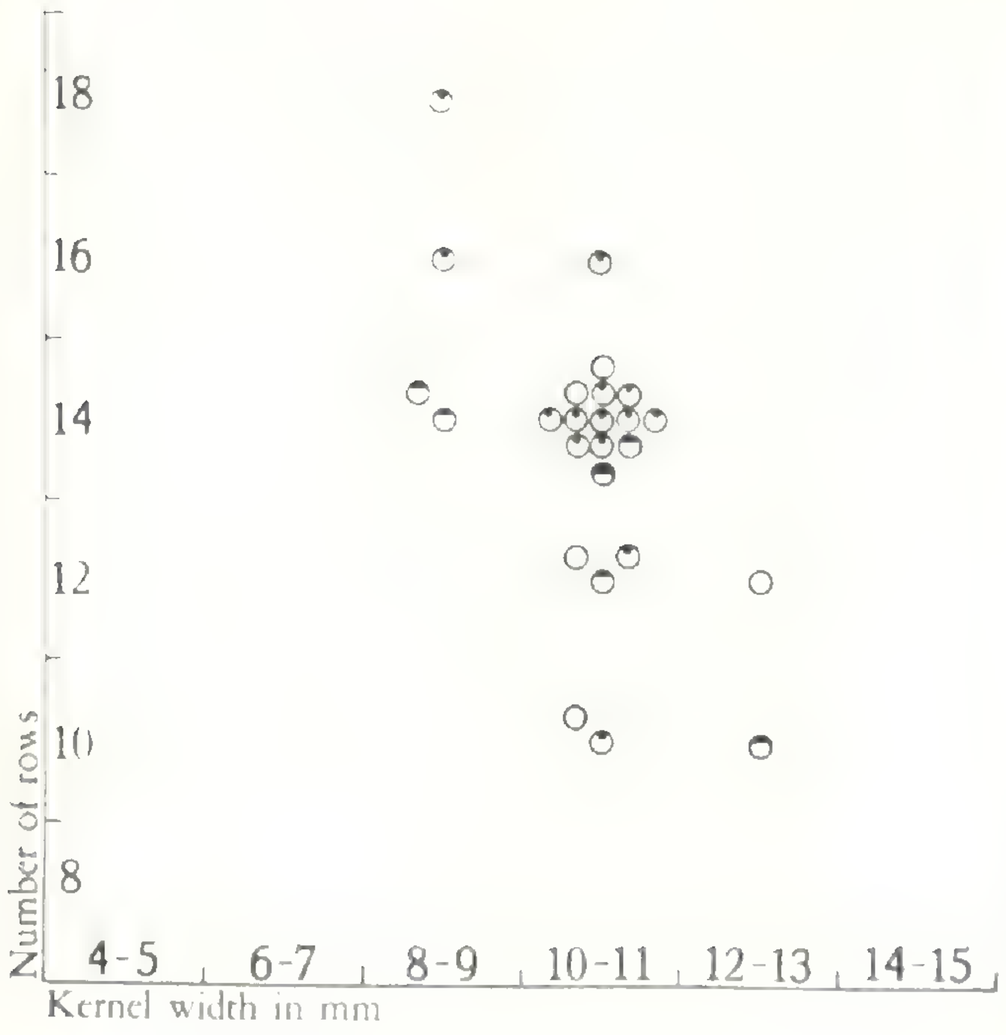
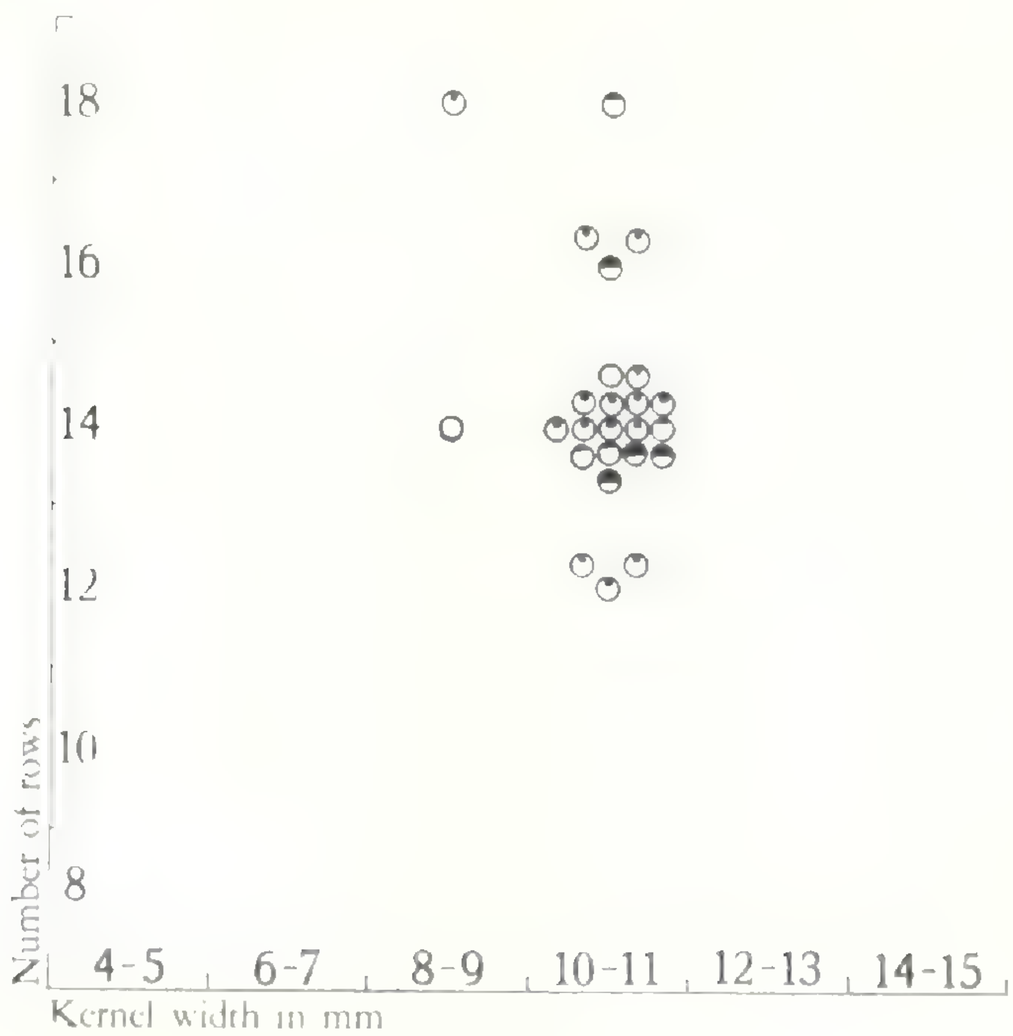


3. San Antonio Aguascalientes

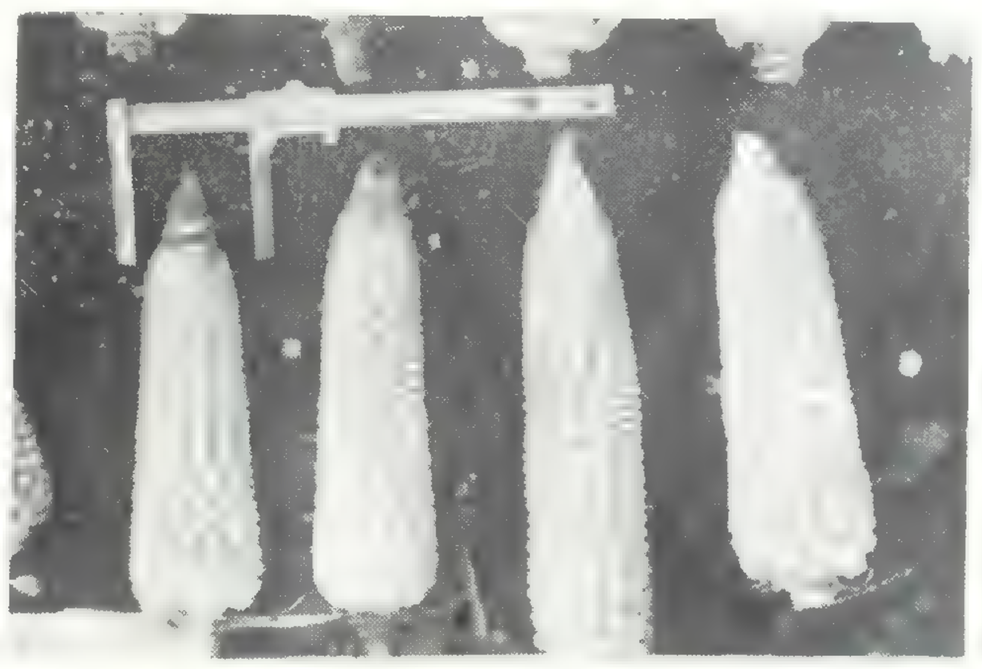


4. Dueñas

3. Common white corn from the purely Indian village of San Antonio Aguascalientes. The corn from this same crib is shown in text-fig. 2. All white cobs. Fourteen ears showed a few yellow kernels, 7 a few with colored endosperm (Pr). Colorless pericarp throughout.

4. White corn from Dueñas. Most of the cobs were light purple, one was deep red, the rest were white. Each of the ears had from few to many kernels with yellow endosperm, 5 ears had a few kernels with colored aleurone (Pr), and 4 had a light flush of color in the pericarp.

3.



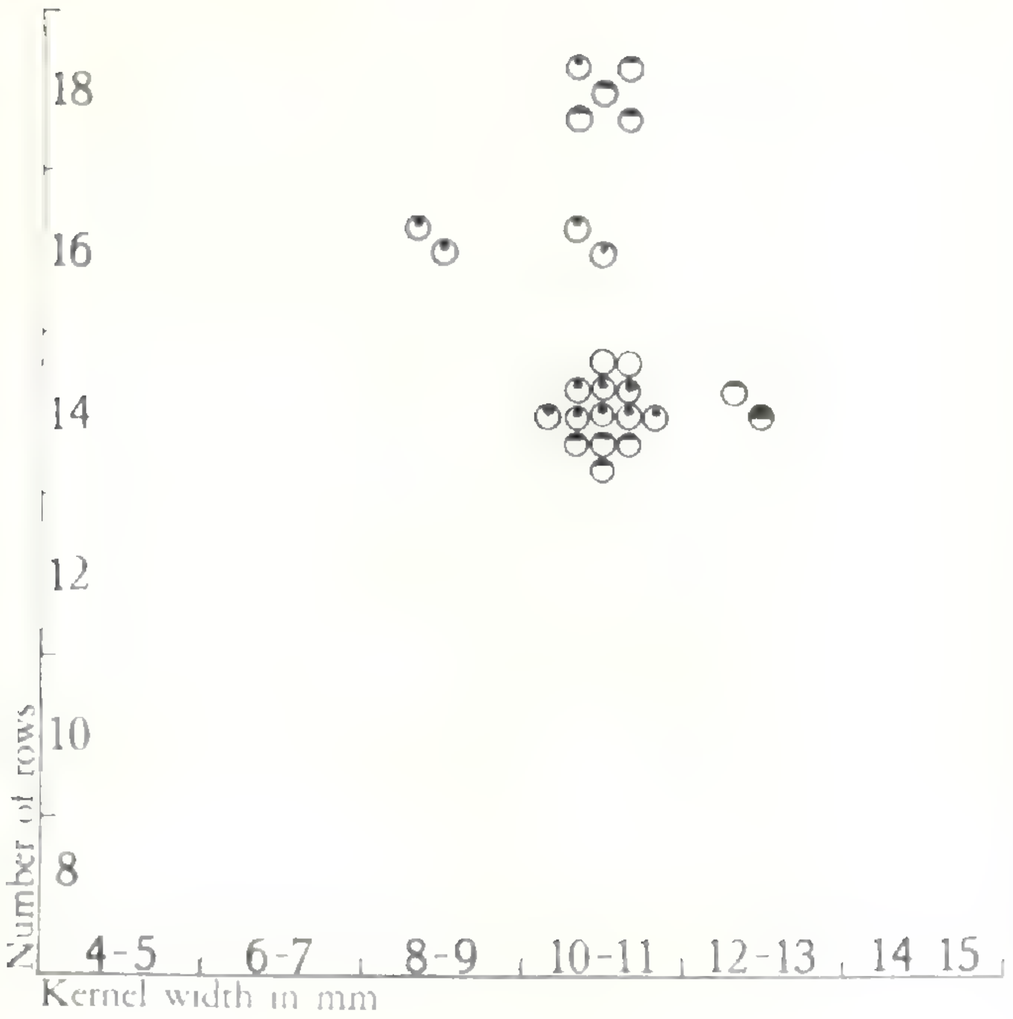
4.

5. Recolección

6. Medio Monte

5. White corn grown by a poor family living in the ruins of Recolección, in Antigua. Only 5 ears were pure white, 7 were predominantly yellow, and the remainder had numerous yellow kernels. Most of the cobs were white, 2 were red and 2 a very faint red. Seven ears had occasional kernels with colored aleurone (mostly Pr, but a few pr).

6. This sample of yellow corn was measured in a small crib in Dueñas though the family who owned it had grown it at Medio Monte. Most of the cobs were white, 1 was deep red, 1 purple, and 5 a very faint purple. Six of the ears were segregating for white kernels, and 2 had a few kernels with colored aleurone (Pr). Five of the ears had a light flush of color in the pericarp.

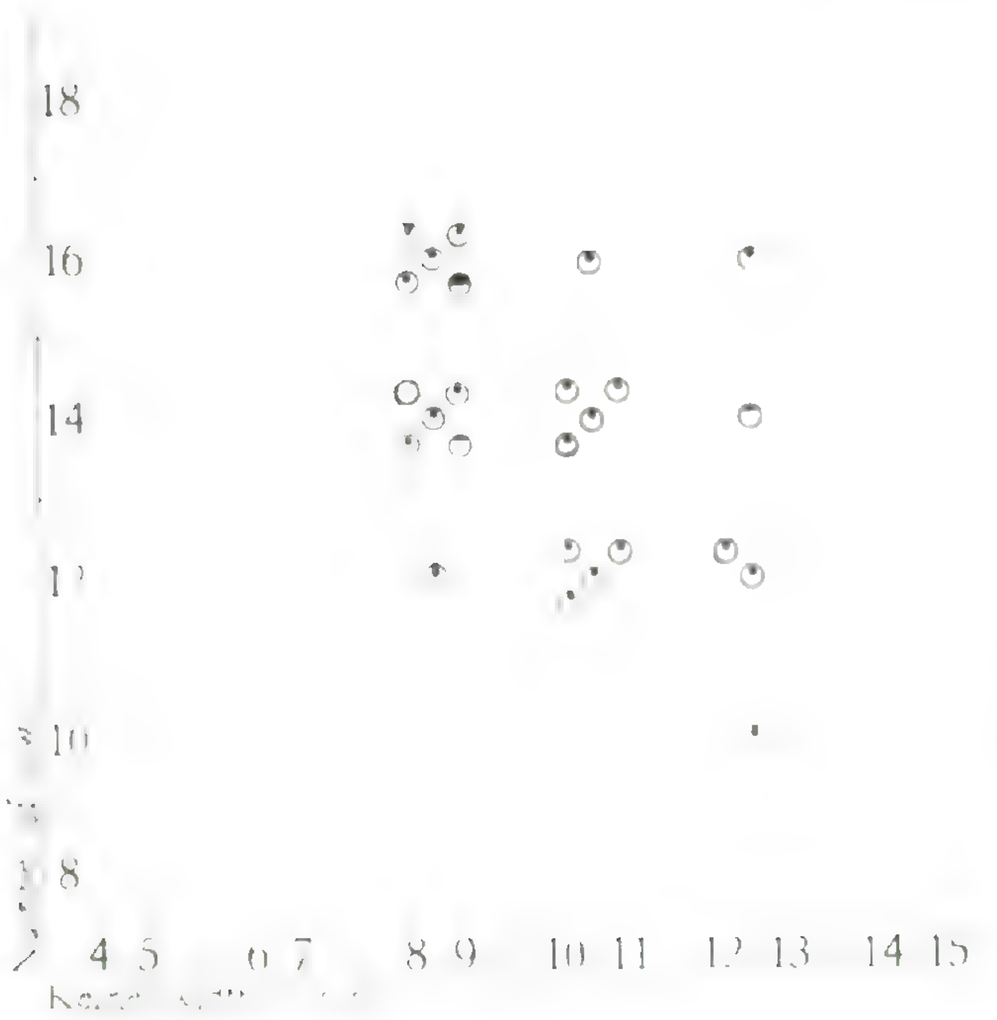


7. Cuidad Vieja

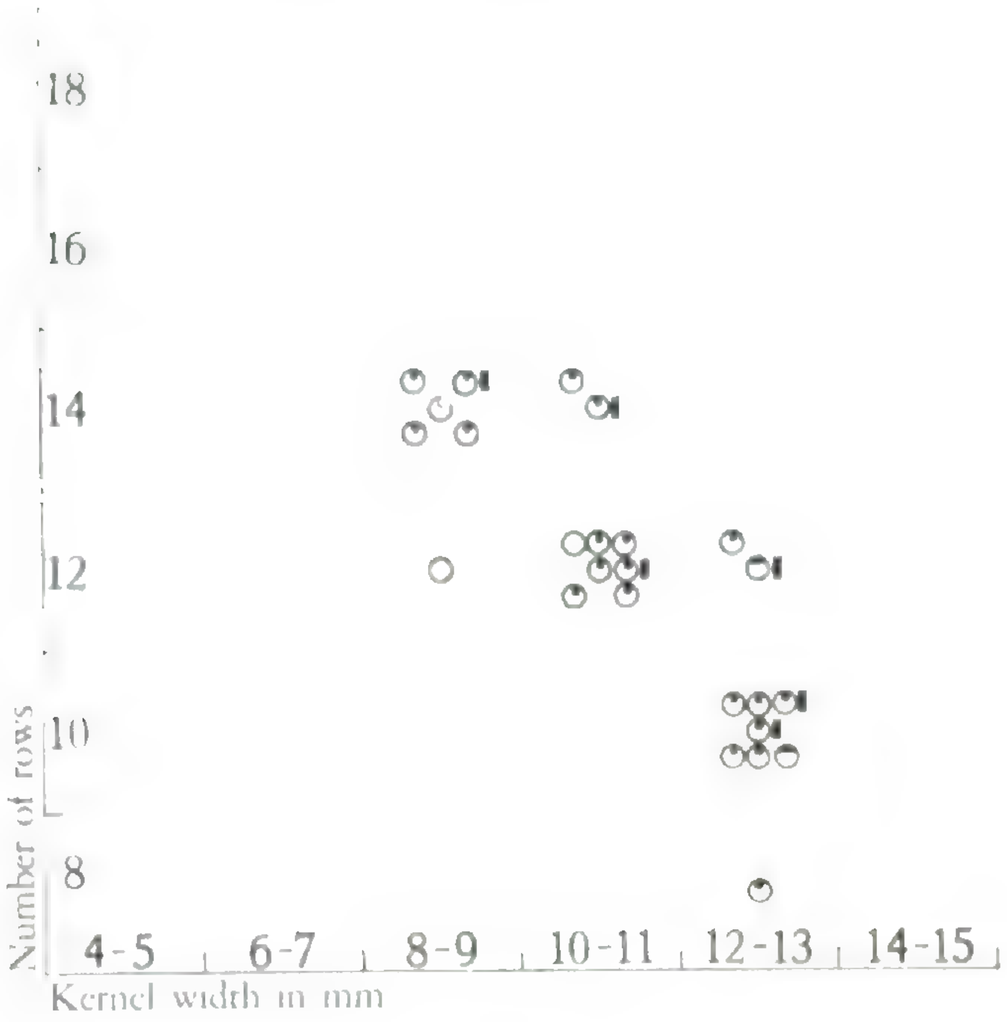
8. Cuidad Vieja

7. Measured at Cuidad Vieja. Thirteen of the ears had purplish cobs, the rest were white. One ear had a few yellow kernels, the remainder were all white. Four ears had a few kernéls with colored aleurone (Pr), and 3 had a faint flush of color in the pericarp.

8. Grown by the same family which grew No. 7 but at another location. White corn, nine of the ears with a few yellow kernels. Seven ears with light purplish cobs, the rest white. Six ears had a few kernels with colored aleurone (Pr) and 2 had a faint flush of color in the pericarp.



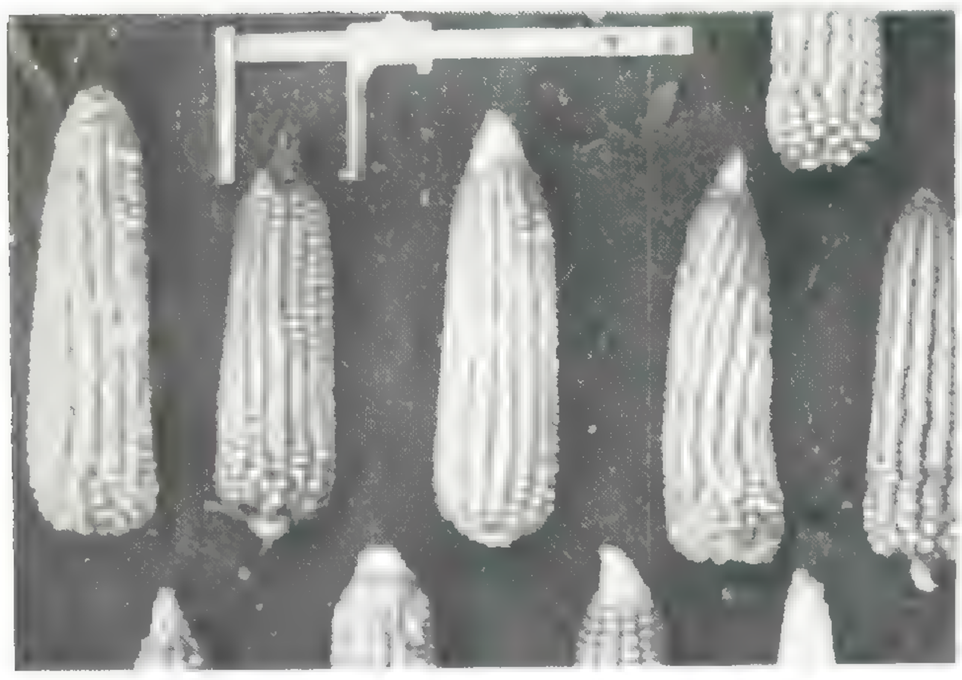
9. Dueñas



10. Santa Lucía

9. Dueñas. All of the ears with white endosperm. Five of the cobs were purplish, the rest were white. Thirteen of the ears had a few kernels with colored aleurone (Pr) while 3 had a faint flush of color in the pericarp.

10. "Maiz haujaqueña", white corn from Santa Lucía above Antigua (see also after No. 10a). Nearly all the ears had a few yellow kernels. Three ears had a single kernel with colored aléuronė (Pr). None were flushed with color in the pericarp, and only one showed faint purplish on the cob. Six ears had been selected for seed (indicated by a bar on the diagram).



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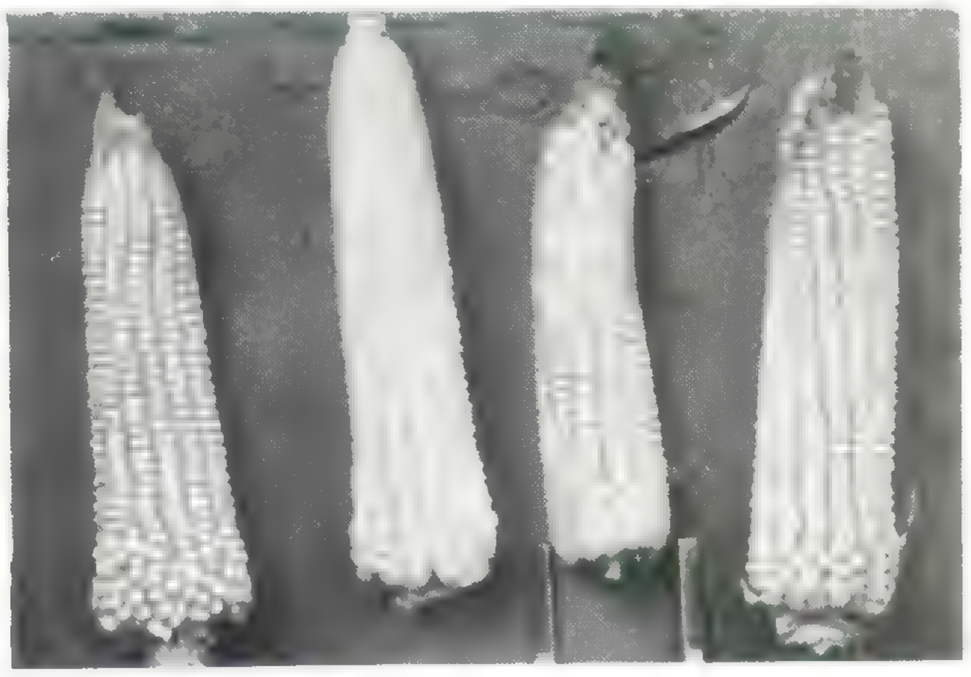

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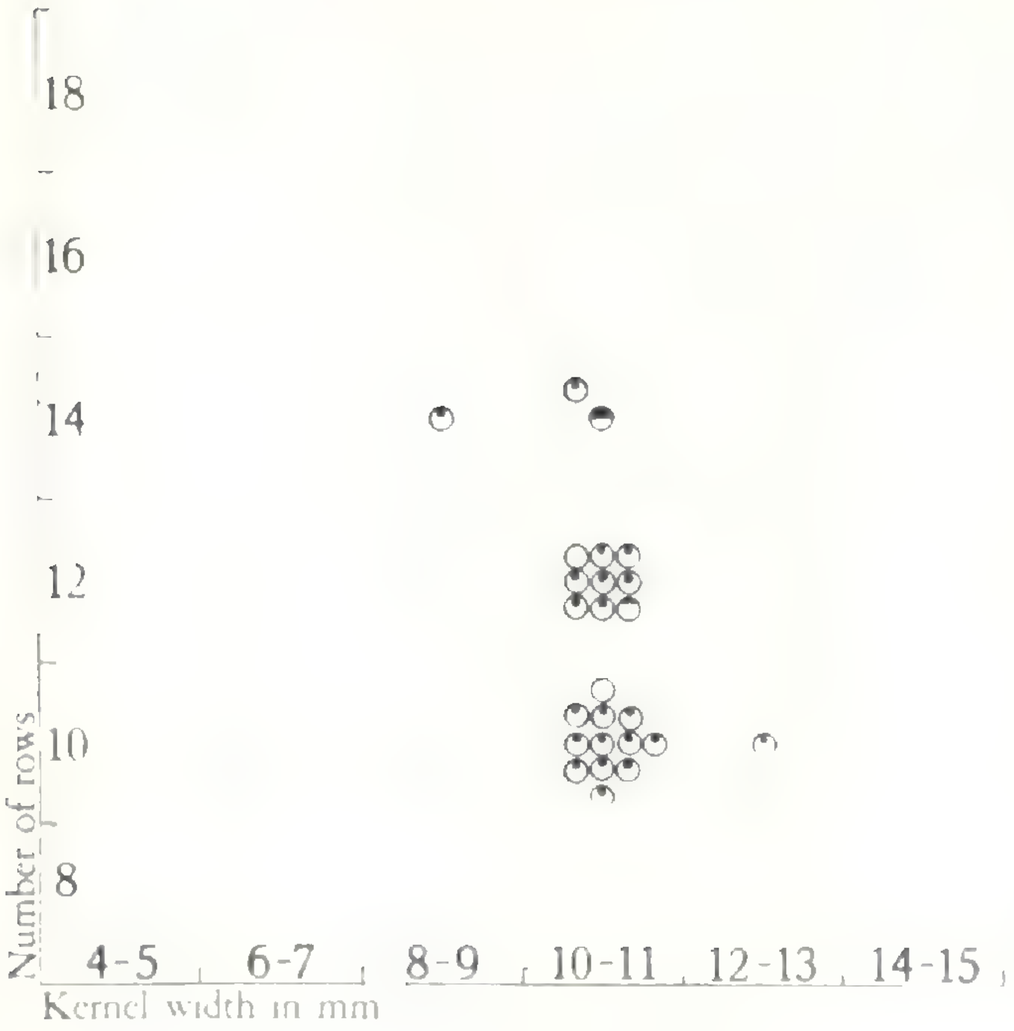


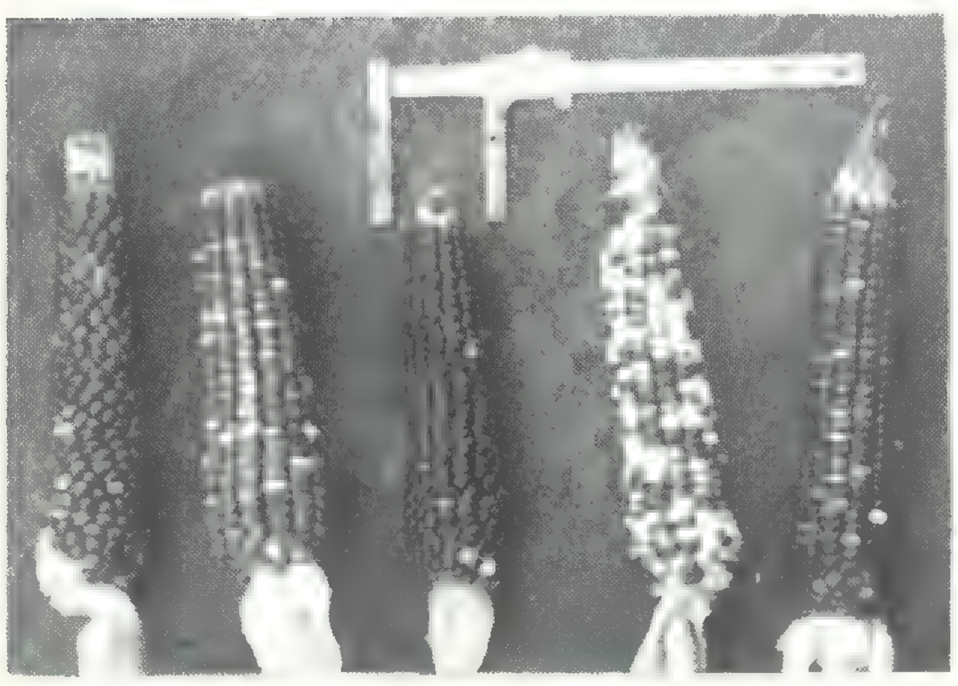
11. Santa Lucía

12. Santa Lucía

11. "Maíz negrito". Santa Lucía. The great majority of the ears had dark blue aleurone (Pr), most of them with an extensive admixture of white kernels. On 4 ears a few kernels had red aleurone (pr). Seven of the ears had some kernels with yellow endosperm, 6 of them had a faint flush of color in their pericarp, and one had a finely variegated pericarp (some allele of P).

12. Yellow corn from the same family. Five ears had faint purplish cobs, the rest being white. All the ears had yellow endosperms, 4 had few to many white kernels. Three had a flush of color in the pericarp, 2 had fine variegation (allele of P). Five ears (marked with a bar) were nubbins ("Mulcos").

(**10a** is a snapshot of the same white corn as No. 10, taken at the open door of the corn crib).



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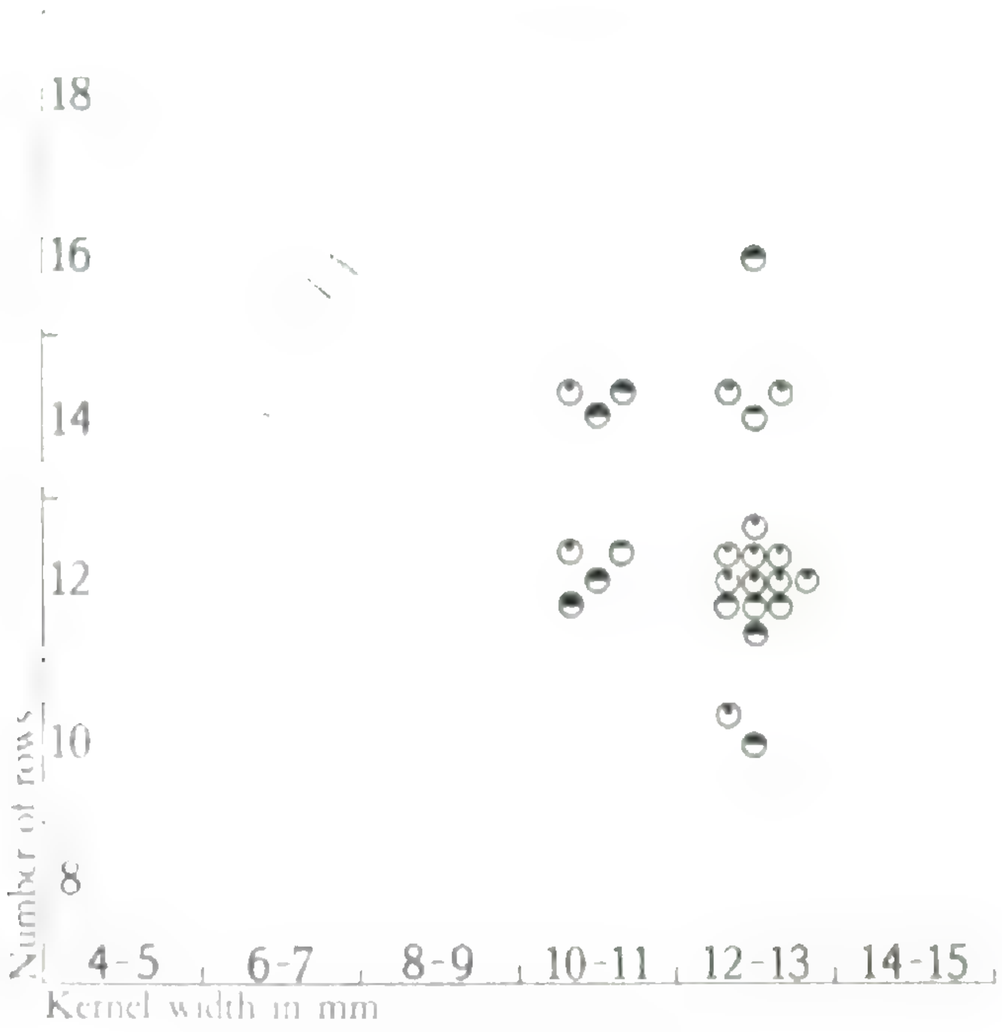
10a

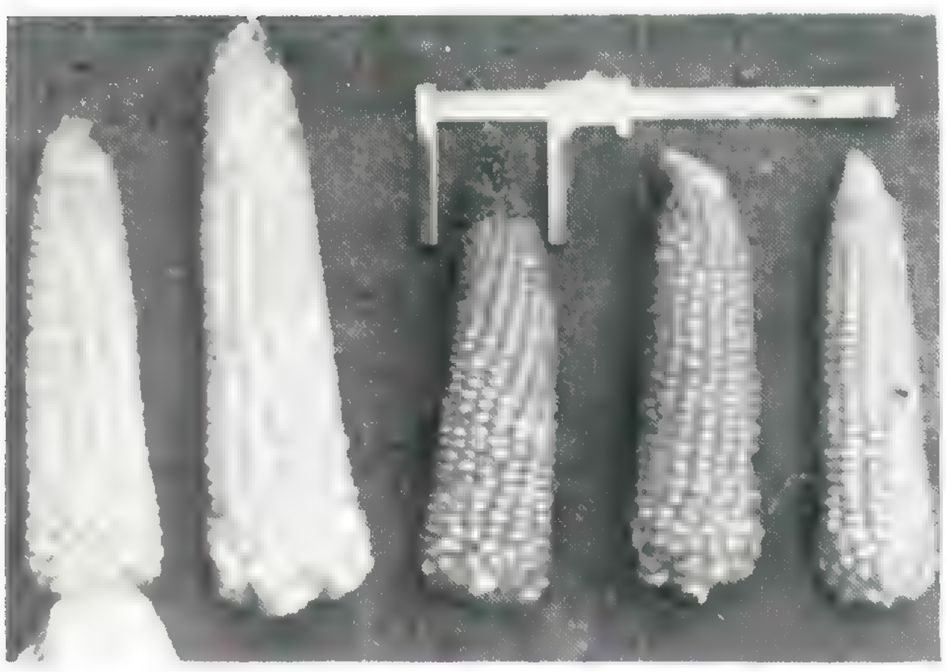
13. San Juan de l'Obispo



14. San Juan de l'Obispo

13. Yellow corn from San Juan de l'Obispo. Some of the ears had a few white kernels, and 4 were segregating for light yellow endosperm. One had a purplish cob; the rest were white. Five of the ears had a few kernels with colored aleurone (Pr), and 4 had a variegated pericarp (allele of P).

14. Blue corn from another family in San Juan de l'Obispo. All but one of the ears had dark blue aleurone, many of them segregating for white. The other ear had red aleurone (pr) as well. Most of the ears had some kernels with yellow endosperm, 7 had a flush of color in the pericarp, and one had variegated pericarp (some allele of P).



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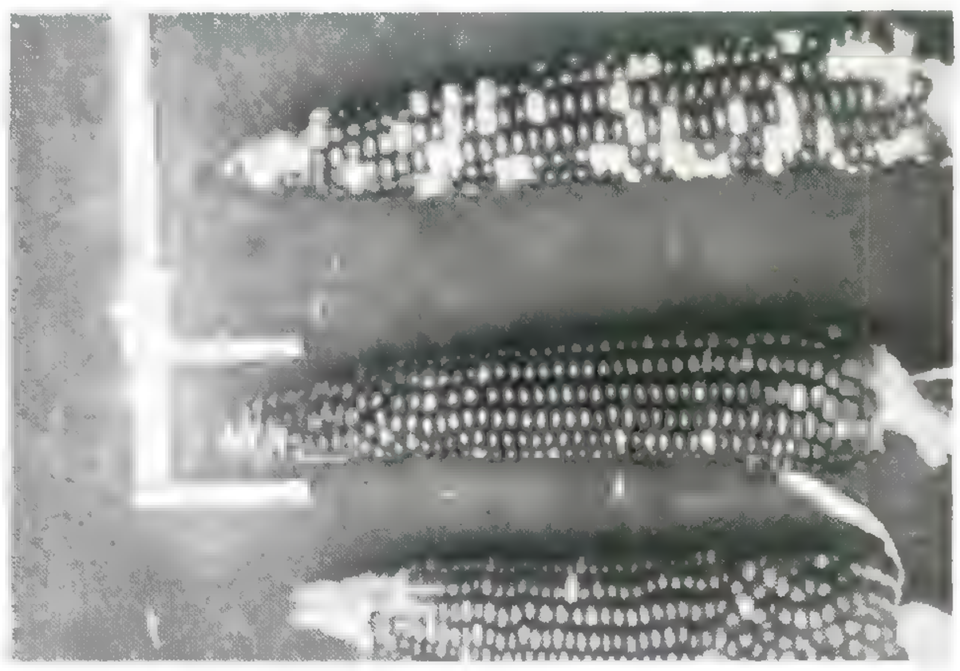
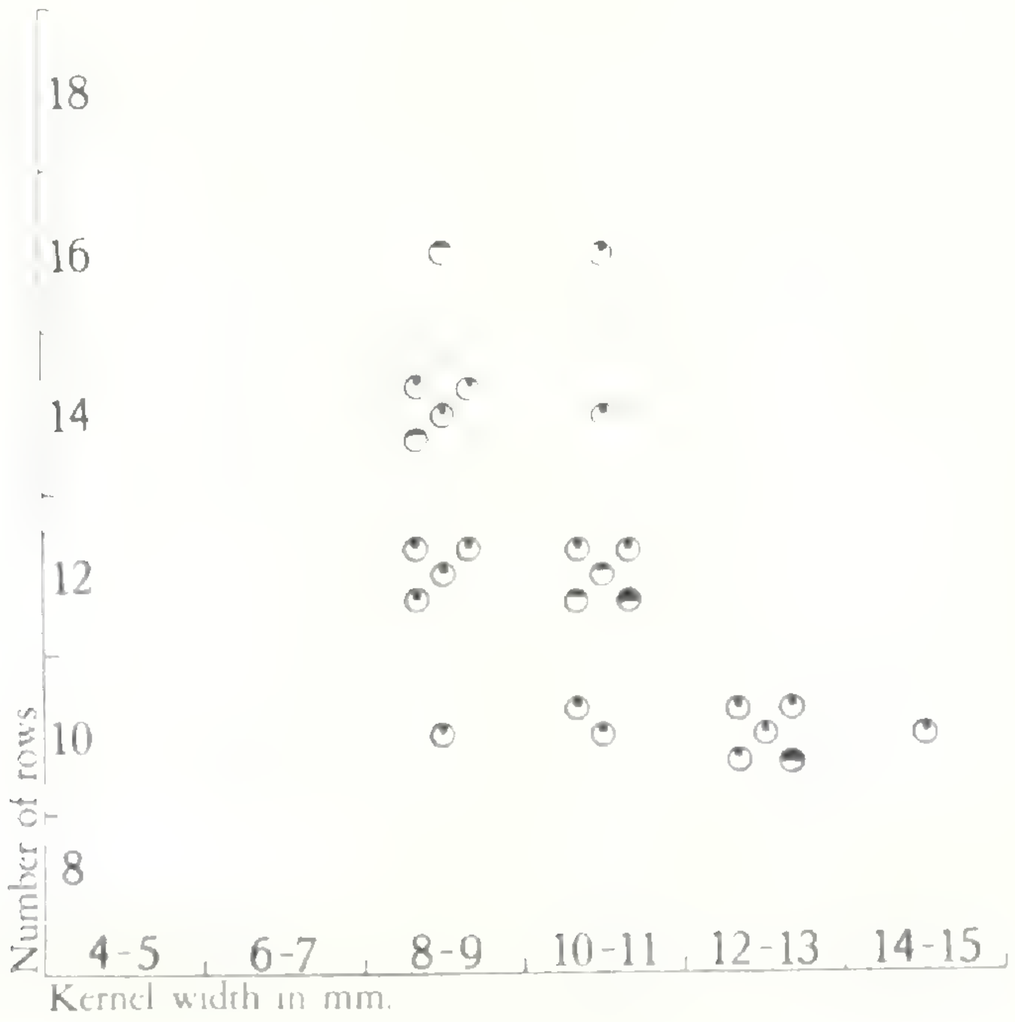


14.

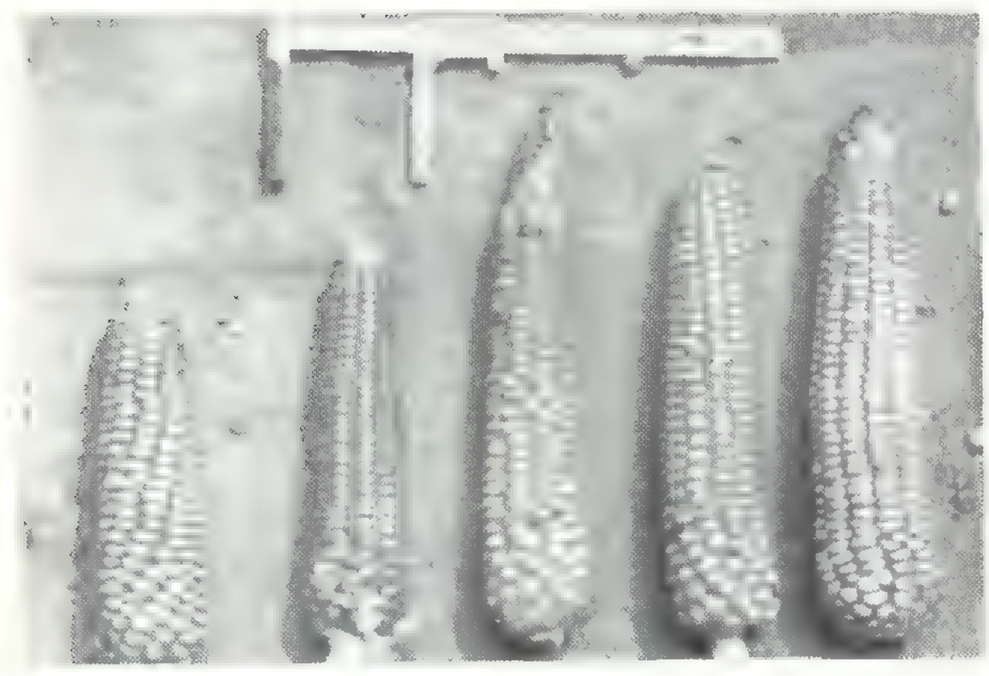
15. San Lucas



16. San Lucas

15. Yellow corn from San Lucas. Most of the cobs were white, 3 being light purple. Nine of the ears had a few kernels with colored aleurone (Pr), 1 had a flush of color in the pericarp, and 2 had red pericarp with a colorless "crown" (P^{cr}).

16. Blue corn from San Lucas. Photographed on the drying floor; not to the same scale as the other photographs. Most of the cobs were white, 2 being pale purple. Most of the ears had a few to many yellow kernels, 7 had a flush of color in the pericarp, and 1 ear had fine stripes of red from some allele of P. All the ears bore colored aleurone (Pr), usually with some white kernels. One ear had red aleurone (pr).



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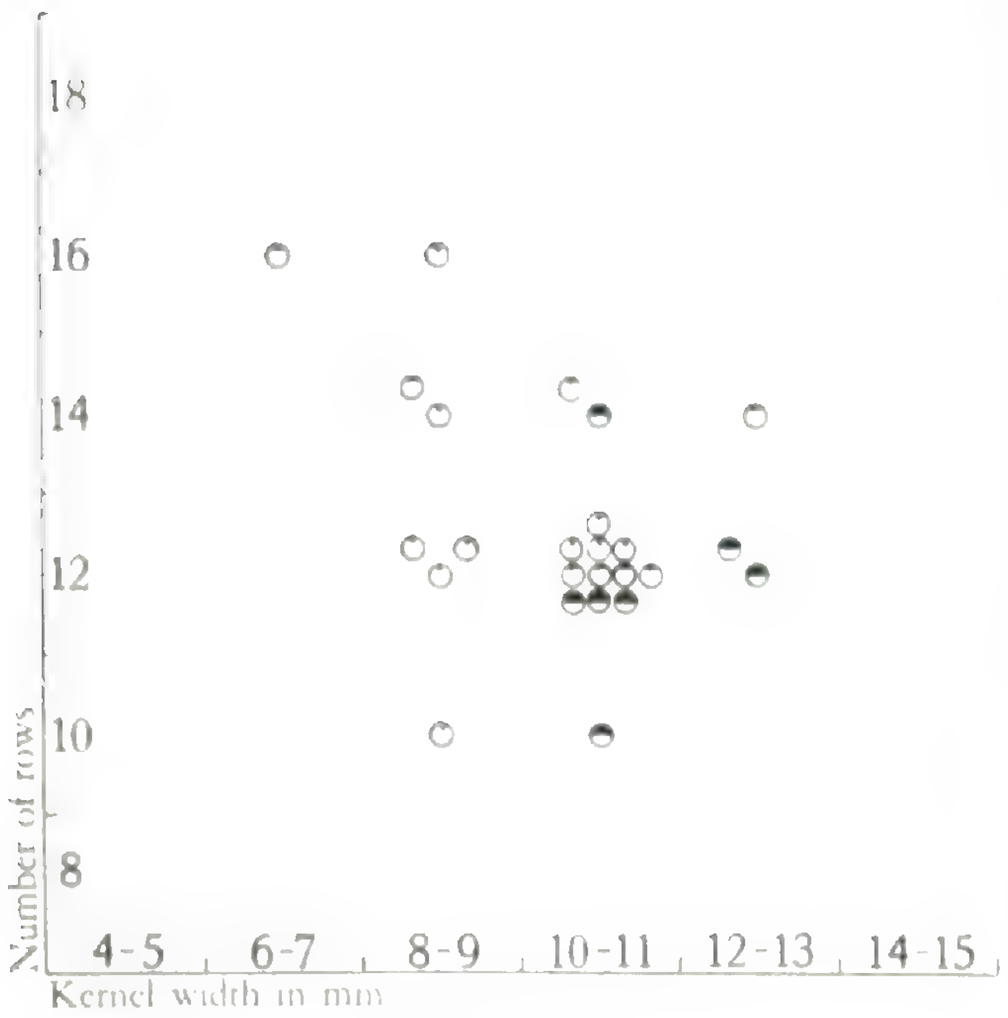
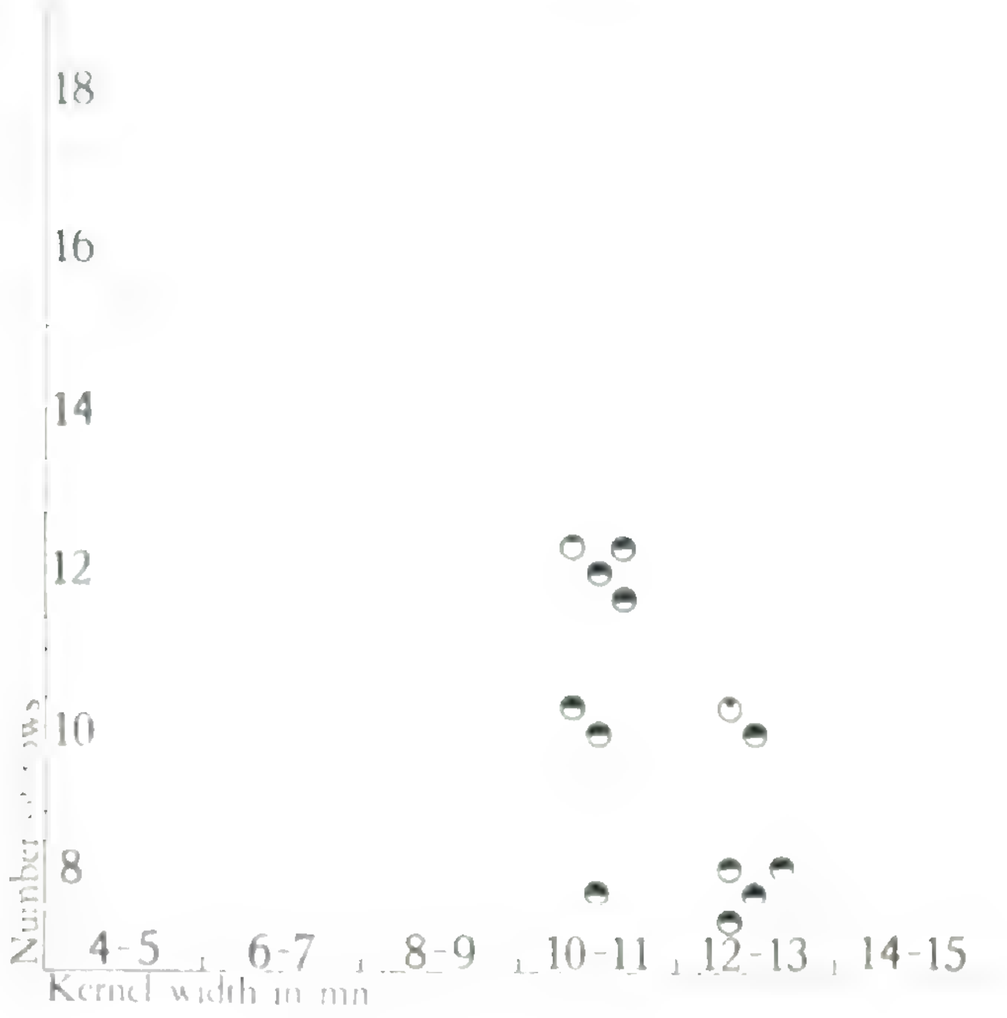


17. Chimaltenango

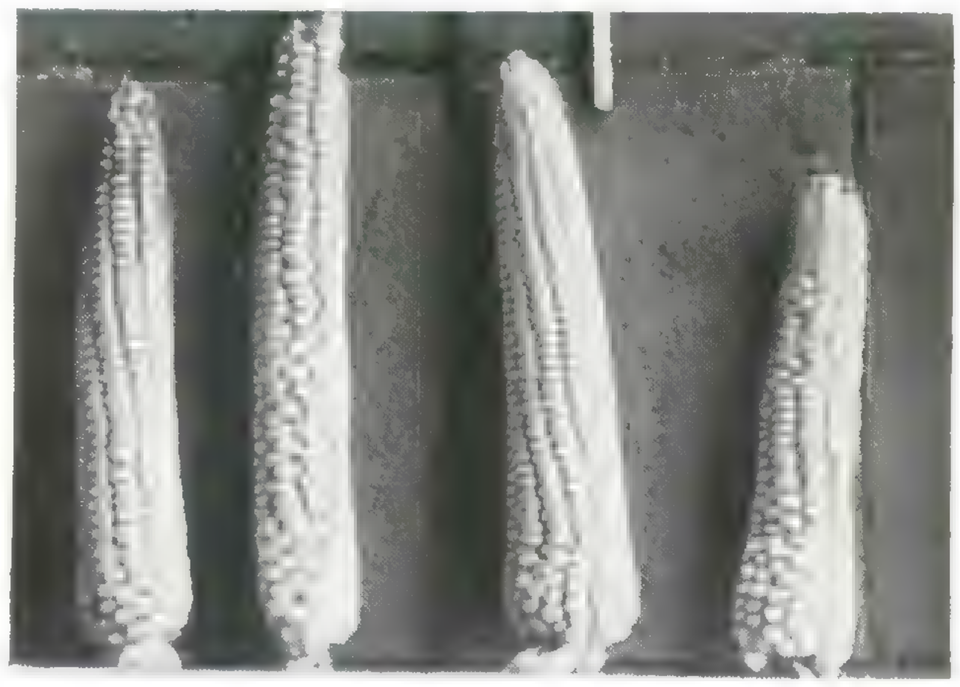


18. San Miguel Morazón

17. A very mixed yellow corn growing at a third-rate hotel in Chimaltenango. Seven of the ears were segregating for white. The cobs were mostly white, 3 being faint purple, and 2 variegated red and white. Four of the ears had some kernels with colored aleurone (Pr).

18. A distinctive variety from San Miguel Morazón, grown 500 feet above the town itself. Combines a white kernel and low row numbers. Not a random crib sample. All ears with white cobs, 4 with a few yellow kernels, 3 with occasional kernels of colored aleurone (Pr).

17



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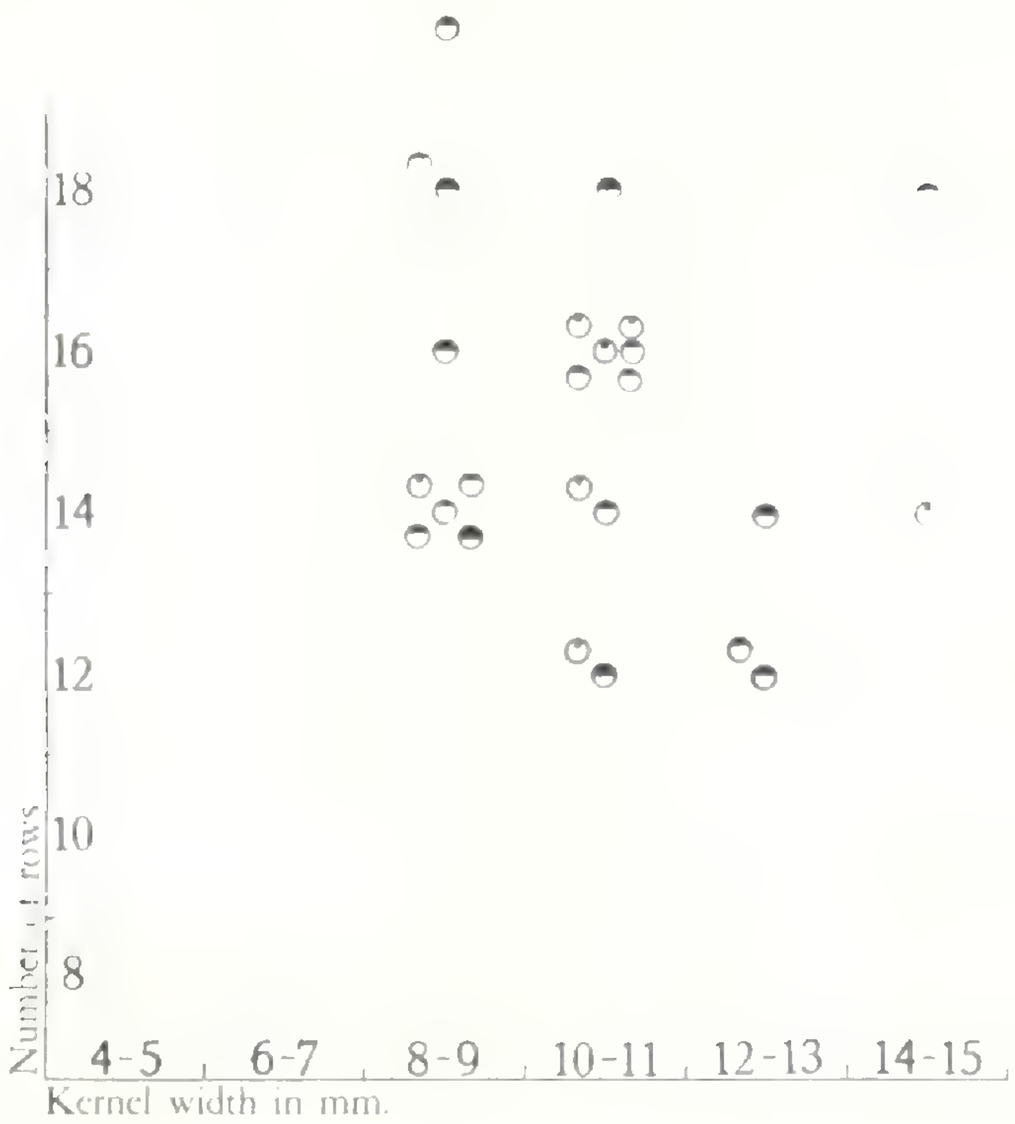
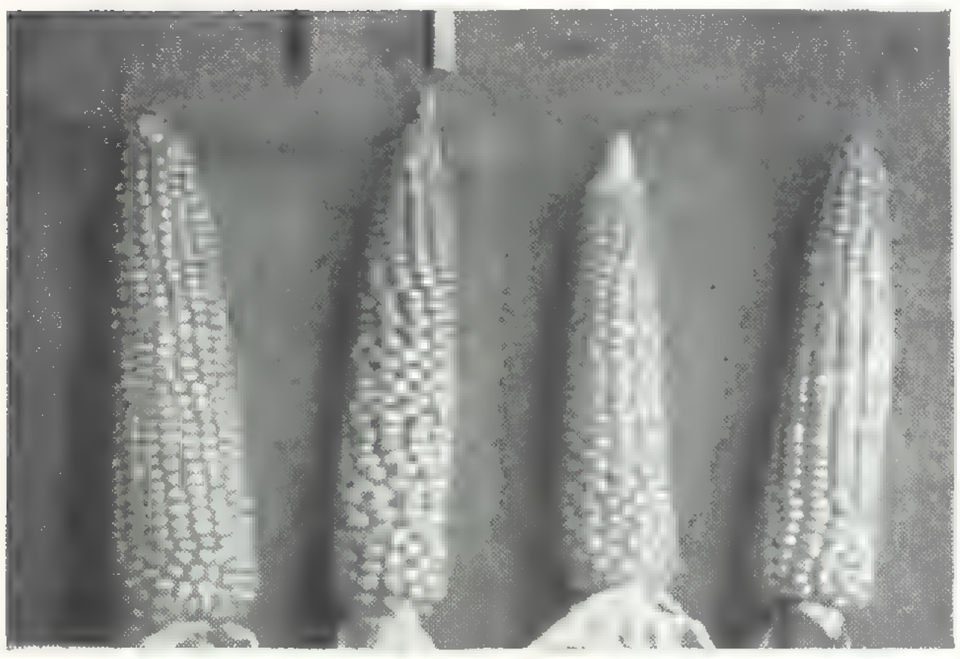
19. Paramos



20. Paramos

19. Yellow corn from near Paramos. Two ears showed a few white kernels, 7 had light purple cobs, 1 had deep purple. This and the next sample represent high-yielding varieties grown by highly skilled growers.

20. Paramos. Yellow corn, 6 ears segregating for white, 1 segregating light and dark yellow. One cob was deep purple, 7 a faint purple, the rest all white. Three ears showed a few kernéls with colored aleurone (Pr).



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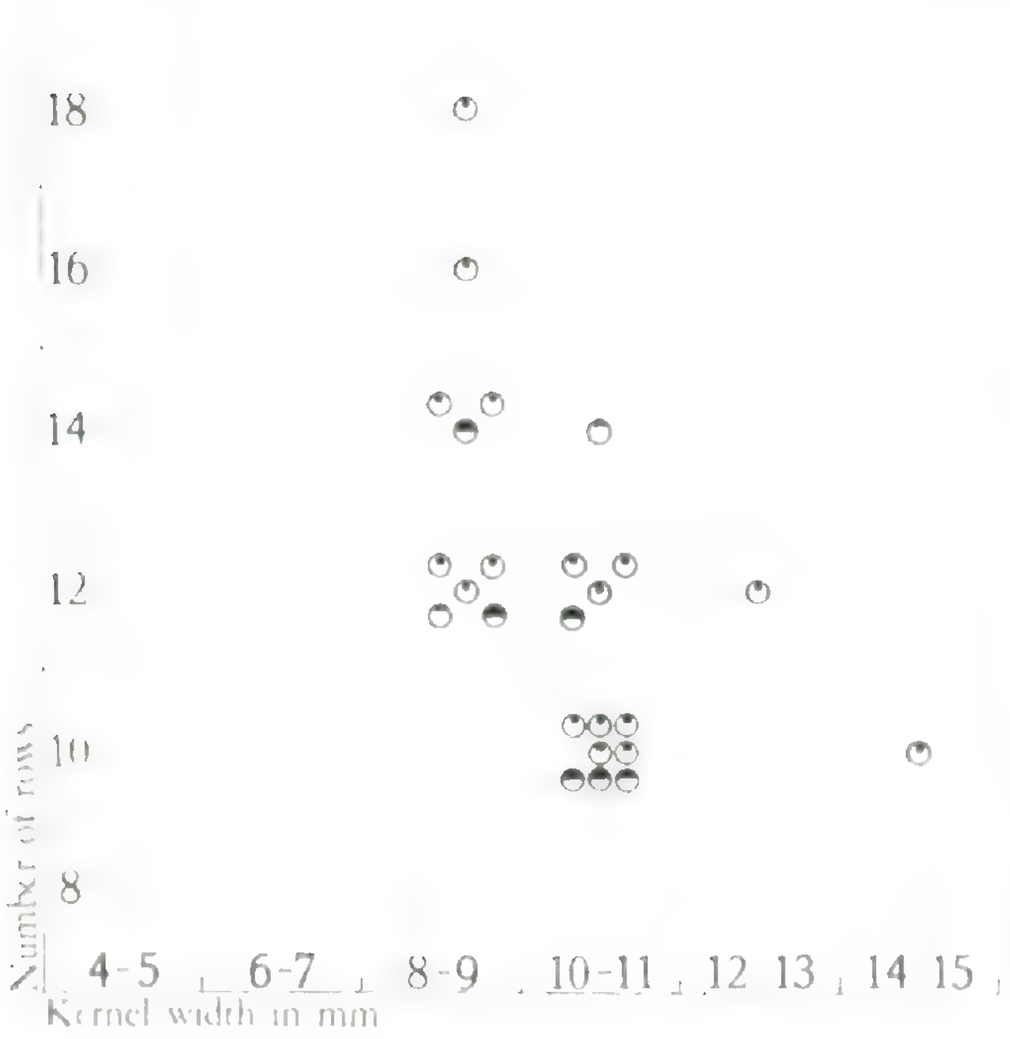
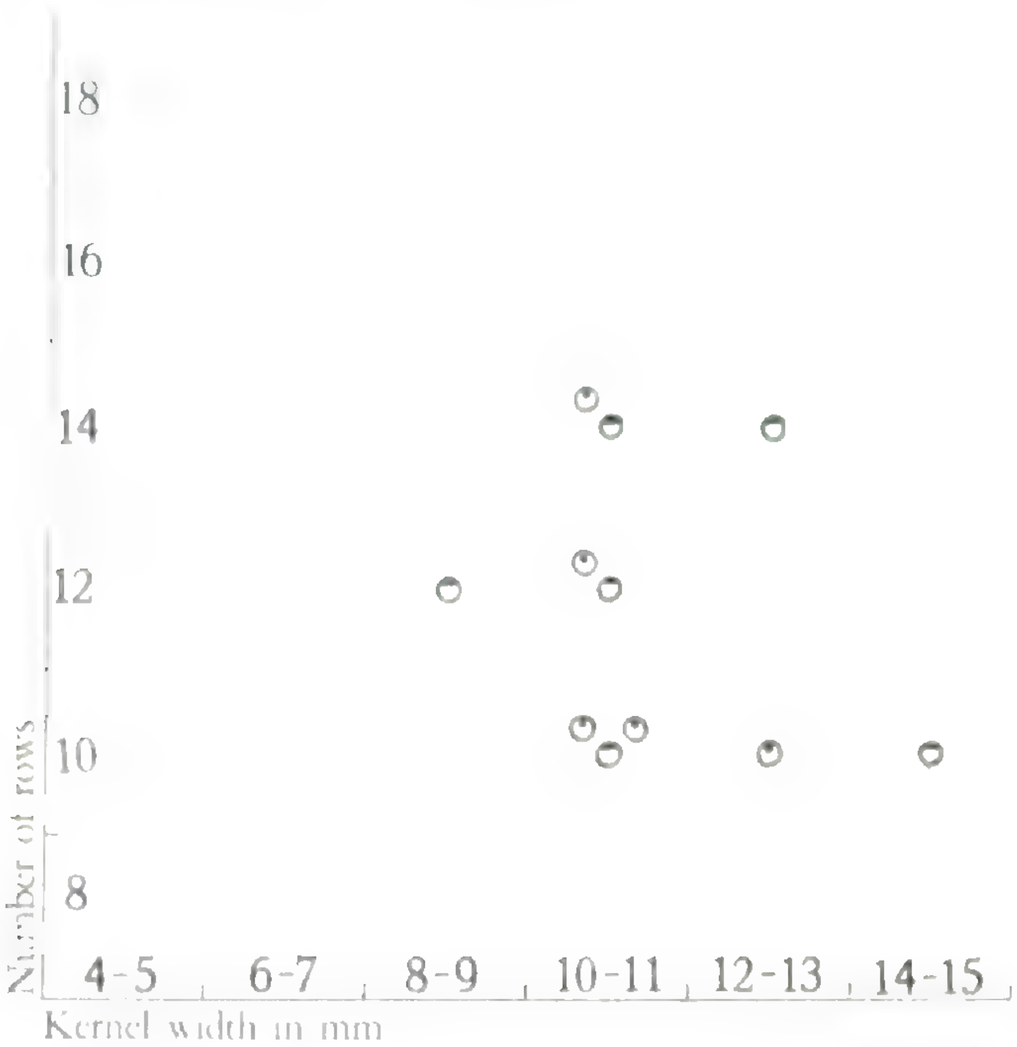


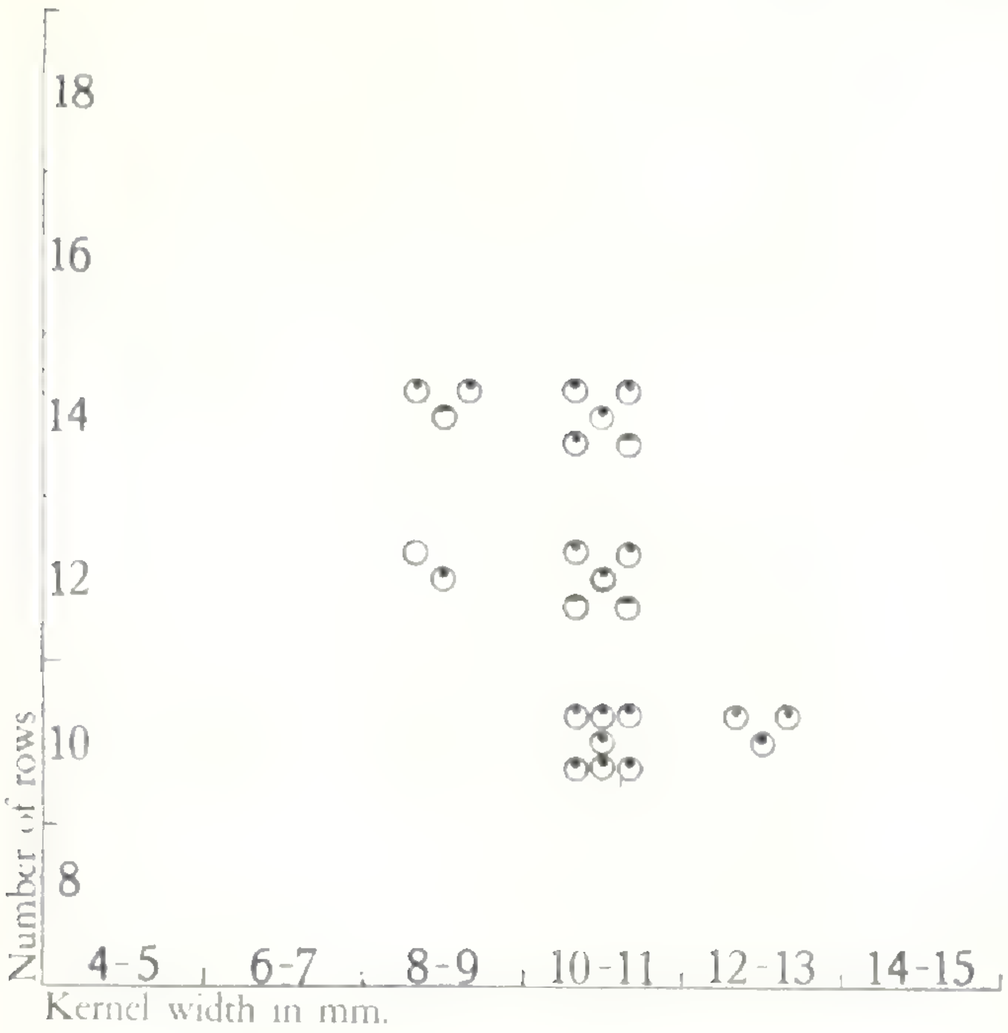
21. Mixco



22. High above Zuñil

21. Yellow corn from a small ranch maintained as a show place by a Guatemalan industrialist. Six ears were segregating for white, 4 had a few kernels with colored aleurone (Pr).

22. High above Zuñil. Due to the high altitude and steep-facing north slope, this corn was only partly ripe on December 14. The 11 ears represent all the mature ears in a small field. Six had white cobs, 3 variegated, and 1 light purple. Seven showed variegated pericarp (some allele of P) and 1 had a flush of color. Nearly all the ears showed at least a little multiplication.

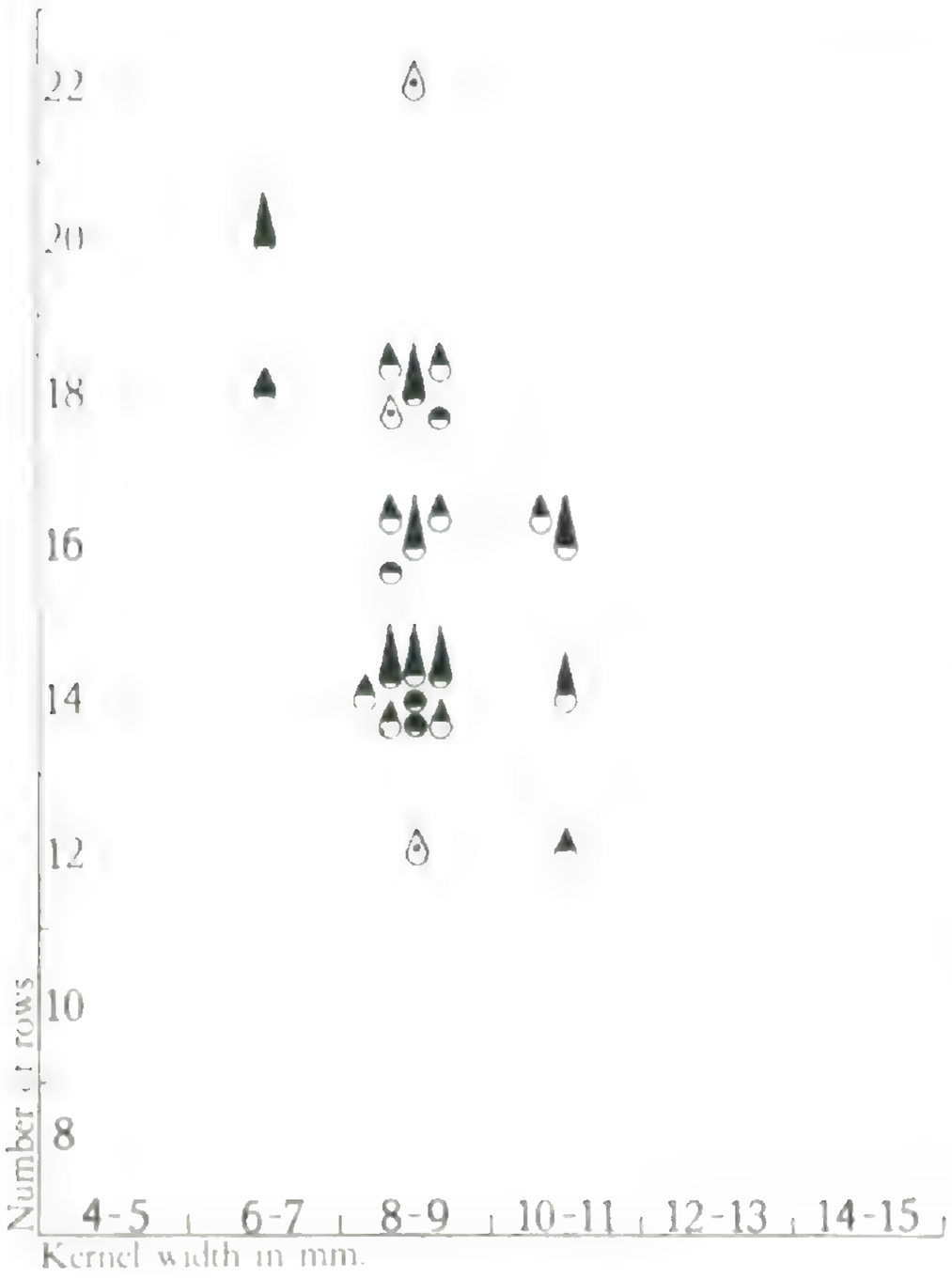


23. Above Zuñil

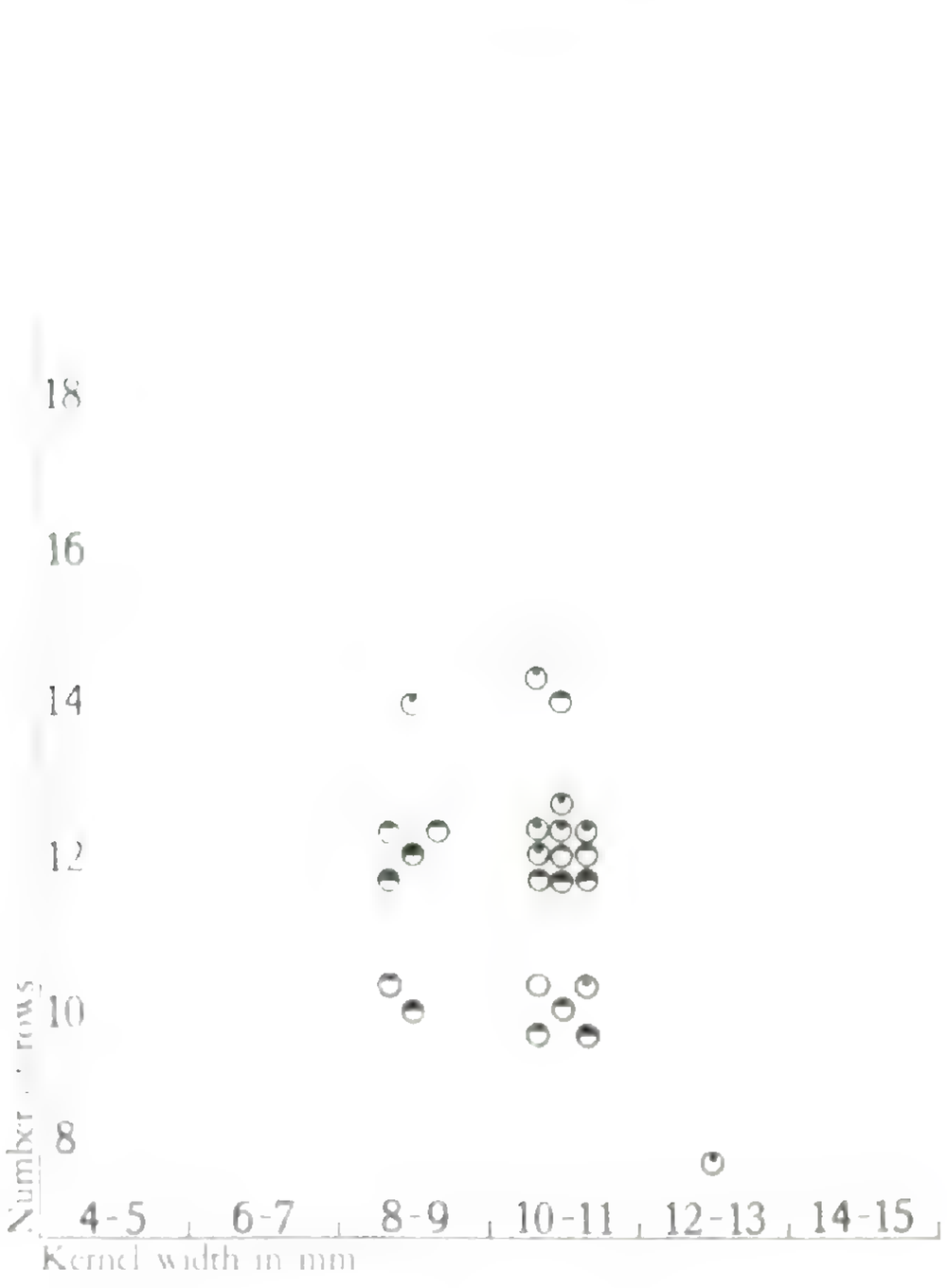
24. Above Zuñil

23. Above Zuñil. Grown half a mile straight down the slope from the 11-ear sample. Just barely ripe December 14. Three had faint purple cobs, the rest were white. All had yellow éndosperm. None had colored aleurone, 6 of the ears had a faint flush of color in their pericarp. Though grown by a non Spanish-speaking Indian, the variety was very uniform.

24. White corn, above Zuñil. Grown by an Indian who lived on the same mountainside from which the 2 samples of yellow corn were obtained. Pictures of the corn on the drying floor are shown in text-figs. 3 and 4. Though prevailingly a white variety, good ears with colored pericarp were apparently being included in the seed selection for next year. Twelve of the ears are a random sample from the drying floor; the other 13 are from the seed ears which had been set at one side (indicated on the diagram by a bar). Four of the ears had light pink cobs (possibly an allele of P). Ten of the ears showed various alleles of P, (P^{cr}, P, etc.).



25. Nueva Cuartel. White



26. Nueva Cuartel. Yellow

25. This and the next sample were grown in the northern edge of Quezaltenango by the same man. This white variety with pointed kernels is similar to many Mexican varieties. It is well known around Quezaltenango, and I have received specimen ears through several different collectors. Twenty-four of the cobs were white, 1 was red. All but 2 ears showed a few yellow kernels, 4 had a flush of color in the pericarp and 1 had a few kernels with colored aleurone (Pr).

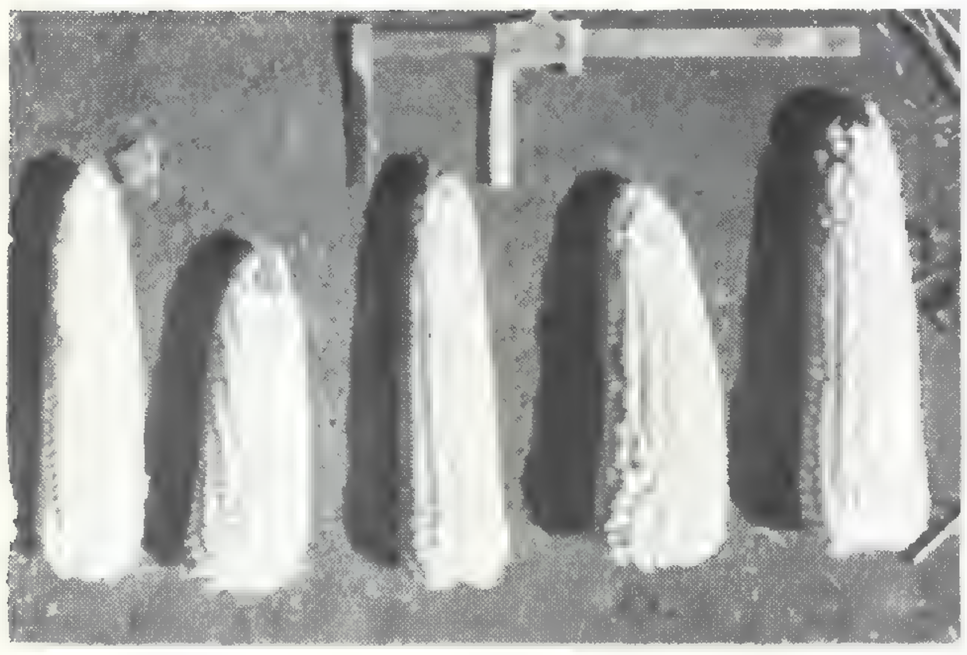
26. Yellow corn. One ear had a red cob, the rest being white. Three ears showed some white kernels, 1 had "crowned" color in the pericarp (P^{cr}), and three a faint flush of color there.

27. Doña Laura, Quezaltenango

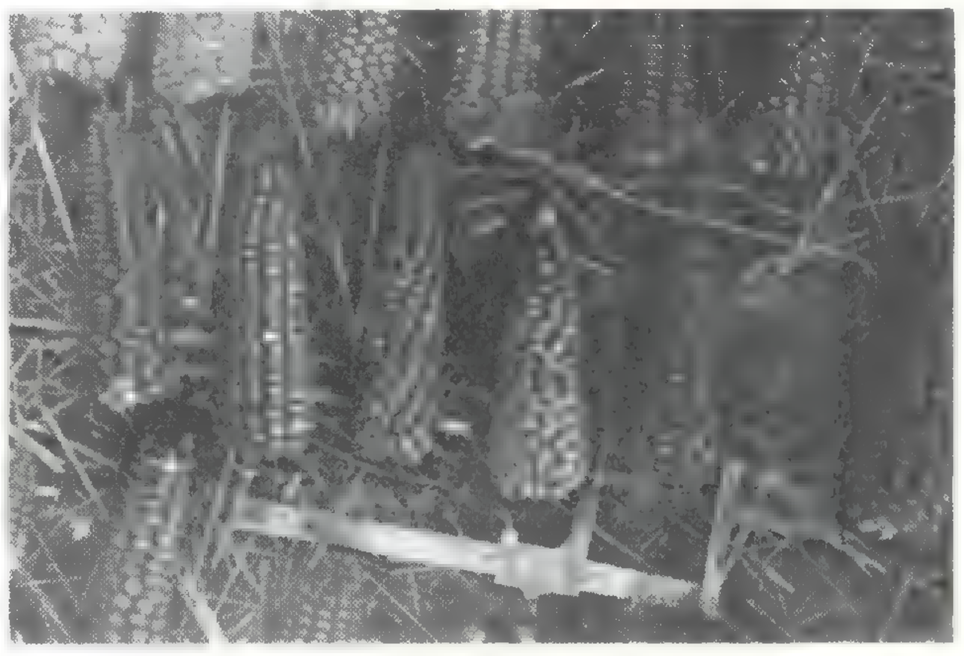
28. Doña Laura, Quezaltenango

27. This and the following represent second-class varieties grown on a farm given over very largely to wheat. The owner had taken relatively little interest in the corn and it was rather mixed. Seven ears had few to many yellow kernels, 5 had a flush of color in the pericarp, and 1 had a faint purple cob. Three of the ears showed multiplication.

28. Yellow corn from the same farm as No. 27. One cob was red, 4 were faint purple. Two had flushed pericarp, 10 showed multiplication.



27



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